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Effects of random mating F2 populations of maize

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Effects of random mating F_2 populations of maize

by

Jorge Covarrubias-Prieto

A Dissertation Submitted to the
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Iowa State University
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TABLE OF CONTENTS

INTRODUCTION

The improvement for some traits was quite rapid in the first stages of corn (Zea mays L.) breeding, because the variability within the landrace cultivars available to the corn breeders was greater than in the populations used today. To attain the same level of improvement, the breeder needs to spend greater effort because the sources of germplasm have become more restricted than in the past. The level of performance for many characteristics has been improved through the history of corn breeding. The elite lines developed by pedigree selection have desirable characteristics, but the genetic variability has been reduced. The same gene pool background is shared among many of the populations used in breeding programs.

Most of the U. S. corn breeders emphasize pedigree selection in F_2 populations derived from crosses among elite inbred lines. They desire to isolate segregants that have a combination of the favorable characteristics of both parents. In these instances, the genetic variability is limited, and the chances for favorable recombinants are limited because no opportunities for additional recombination are permitted. Relative to the total effort, little attention is given to breeding methods that include recombination, such as recurrent selection. Very few recurrent selections are conducted in applied breeding programs that emphasize line and hybrid development. Corn breeders also do not give much attention to the effects of random mating after the cross of two homozygous lines to increase the frequency of recombi-

nant genotypes.

The expected favorable effect that the breeder would expect with random mating is the breakup of linkage blocks that are maintained intact without recombination. The occurrence of some recombinants among selected progenies from crosses of elite lines is crucial to corn breeders for the success of their programs. The breakup of linkage blocks and the recombination of desirable genetic types can be achieved after several generations of random mating.

The main objectives of this study were:

1. To determine if random mating promotes an increase in the range of transgressive segregates in the F_2 generation of two single crosses developed from crosses of related and unrelated inbred lines;
2. To determine if the mean of F_2 generations of four single crosses is affected after by random mating;
3. To determine if the breakup of linkage blocks can be increased as measured by the changes in the genetic correlations among traits; and
4. To determine if random mating after the cross of two homozygous parents could be considered a good practice before initiating selection.

LITERATURE REVIEW

The more useful procedures in corn (*Zea mays* L.) breeding programs are usually based on the principle of selection within an F_2 population of a cross between two elite lines that generally complement each other for characters of interest. The breeder is looking for recombinant characters in the F_2 generation and, by selfing, to fix desirable genes in homozygous inbreds. This procedure of crossing selected germplasm and selecting in the segregating generations before the evaluation of the inbred lines in specific combinations is repeated for each cycle of pedigree selection. This procedure limits the opportunity for desirable recombinations among linked genes because of the rapid approach to homozygosity (Humphrey et al., 1969).

A possible solution to this problem has suggested random mating of individuals in the F_2 generation for some generations, after which the selfing and selecting procedures can be initiated. There are few studies that have reported on the feasibility of using random mating as a useful procedure in applied breeding programs. Most reports are based on simulated studies. In corn, as far as known, the feasibility of the random mating F_2 populations before initiating selfing and selection has not been investigated.

The main objective of the random mating is to promote the breakup of the linkage blocks that occur when crossing genotypes that differ for several traits. Hanson (1959a), in a theoretical study dealing with chromosome lengths, reported that the population means will not

change in linkage disequilibrium. He also stated that the genetic variability can be inflated as compared to that expected for linkage equilibrium. This aspect of the genetic variability is of great importance for breeders because it reflects the potential progress that can be expected from selection among the homozygous progeny. An increase in the genetic variability is expected after random mating is applied to these types of populations.

Hanson (1959b) also reported that the primary breakup of relatively long linkage blocks would occur in the first four or five generations of intermating. He concluded that the linkage blocks are still of appreciable length at this stage, and that it is extremely difficult to breakup linkage blocks for short chromosomes (0.5 centimorgans). He reported a 64% reduction, on the average, in the original linkage blocks after four generations of intermating. Hanson (1959b) concluded that at least one generation of intermating should be included in breeding programs.

Hanson and Hayman (1963) stated that the detection of changes in genetic variability after intermating could be attributed to linkage among loci that affect a character, but they also remarked that a failure to detect those changes should not exclude the presence of linked loci. Similar estimates for imposed generations of intermating indicated an approach to the equilibrium value.

Miller and Rawlings (1967) reported a negative genetic correlation between yield and fibre strength in cotton (Gossypium hirsutum). They observed a limited occurrence of nonparental types in the F_3 progenies

of a cotton cross for which one parent was of interspecific origin. They found that six cycles of 50% outcrossing produced a better source of material for selection, which was attributed to a partial breakup of linkage blocks in the original material. They reported that the genetic variance decreased for six traits for which they suggested that coupling phase linkage was expected to predominate. The genotypic correlations among the traits under study tended to shift toward the values observed in populations assumed to be in linkage equilibrium. They also observed an increase in the mean of the intermated population during the successive generations of random mating.

Baker (1968), in a simulation study where two and nine loci were considered, reported that random mating in self-pollinated species would be affected in different ways, depending upon the linkage relationships. When repulsion linkages predominate, it is expected that random mating will increase the range of the genotypic values and, hence, the genetic variance of the population. On the other hand, with coupling linkages, a decrease in the genetic variance is expected due to a reduction in the frequencies of the more extreme types.

Baker (1968) also reported that in the two loci-case the intermating appeared to be more effective with recombination values of about 0.10, but this effect would be diminisned as this coefficient of recombination increases. For a two-loci repulsion cross, intermating 20 to 30 pairs of F_2 individuals was sufficient to increase the probability of recovering desirable genotypes. The results of the nine-loci case were similar to those of the two loci-case. With recombination values

of 0.20 and 0.30, intermating 30 random pairs of F_2 individuals would be enough to increase the potential for improvement because means and variances in those populations were higher than in the original F_2 populations. He concluded that it was not expected an increase could occur in the average frequency of desirable genes in the truncated portion of the population, but that it would cause a significant shift in the genotypes contributing to that frequency.

It is of importance to take into account the population size because the random effect of genetic drift will negate any advantage of random mating. Hence, small populations should be avoided.

Meredith and Bridge (1971) used two populations derived from a cotton cross to determine if negative correlations between yield and fiber strength could be reduced by random mating. They found small but significant differences between means of the two populations for some traits, which suggested that either the effects of selection or the breakup of linkages in the intermated populations could have taken place. They also observed a decrease in the genetic correlation between lint yield and fiber strength that was attributed predominantly to repulsion phase linkages. The genetic correlations between other traits also were reduced. These authors stated that intermating would produce the most recombinations when linkages were involved, but no genetic advance was expected. Finally, they suggested the use of large populations and less early selection because under the conventional system of breeding very few desirable recombinants were produced.

Pederson (1974) conducted a simulation study in which he evaluated

the worth of intermating with no restrictions in either the length or the number of chromosomes. Genes were assumed to be distributed throughout the genome with no predominance of the repulsion phase linkages. He assessed the value of intermating by comparing the variances between the populations studied. His discussion was based mainly in three situations where intermating could be beneficial: for a character controlled by loci on a single short chromosome segment; for loci distributed over a long chromosome segment; or for loci situated on two or more short chromosome segments. Intermating would not be beneficial for a character controlled by loci spread over three or more long chromosome segments, due to the overriding effect of chromosome reassortment. He stated that is not possible to define which of those situations is more likely in practice, and he concluded it was difficult to generalize on the possible merits of intermating. He proposed the use of directional selection because the results of his study demonstrated that a change in variance is a reflection of a change in the amount of transgressive segregation.

Bos (1977) simulated the effect of intermating before selfing in the cross of two homozygous lines. He evaluated the effect of intermating by computing the expected number of plants with favorable alleles. Bos (1977) concluded that intermating of F_2 plants was not feasible to increase the expected number of plants with the desired genotypes. He also commented that the positive results reported by Miller and Rawlings (1967) and by Meredith and Bridge (1971), opposed to his results, were explained by the fact that those results were based on

observations on segregating generations. Hence, Bos (1977) acknowledged that results obtained from simulation studies were different from those obtained with applied plant breeding programs.

Stam (1977) also conducted computer simulation studies on the effects of random mating in F_2 populations, as compared to selfing. Some of his conclusions were that, during early generations, there is no substantial advantage of random mating over selfing; that the environmental variance tends to give selfing a relative advantage over random mating; that the response in the long run is superior with random mating, especially with quantitative characters; and, finally, when considering one generation of random mating there exists an optimum moment to do it. It seems, therefore, that Stam (1977) is accepting that at least one generation of random mating can be considered a compromise.

Empirical results of the effect of three cycles of intermating in three populations of wheat (Triticum aestivum) were reported by Altman and Busch (1984). They found some changes in means for several traits, but they did not think that intermating could influence mean performance in a consistent manner. In comparisons of estimates of genetic variances, they did not consider recombination to be effective. Some differences for an increase in genetic variances between cycles of intermating were reported, but this trend was not supported when all intermating levels were evaluated. Their results did not preclude the possibility of increased recombination since recombination would not necessarily lead to observable changes for quantitative traits in those populations and large sampling errors were inherent in their variance

estimates. Hence, only substantial changes in genetic variability would be detected. Altman and Busch (1984) concluded that random mating cannot be considered as a primary breeding procedure prior to selection as measured by line performance after the intermating cycles.

MATERIALS AND METHODS

Four single crosses were included as the source populations: B73 x Mo17, B73 x B84, B79 x B73, and B77 x Mo17. B73 x Mo17 is an example that represents the heterotic pattern frequently considered because both lines are unrelated to each other. B73 x B84 is a cross of inbred lines that were derived from C5 and C7 cycles of selection in BS13(HT). B77 x Mo17 and B79 x B73 are intermediate between B73 x Mo17 and B73 x B84 based on their parentage.

The four single crosses were self-pollinated to obtain the F_2 generation. After the F_2 generation, 250 plants were random mated for six generations (Fig. 1). For each generation of random mating, one kernel was taken from each ear and all seeds were bulked to advance to the next generation. Each generation of random mating was designated as a synthetic (Syn) generation.

From the F_2 and the F_2Syn5 generations of B73 x Mo17 and B73 x B84, 100 S_1 progenies were derived to estimate the genetic variance in the F_2 and F_2Syn5 generations. No intentional selection was practiced in selfing the S_0 plants. The B73 x Mo17 and B73 x B84 single crosses were chosen because they represented the biggest contrast (most heterotic and least heterotic, respectively) in their parentage.

The materials developed (random mated generations and S_1 progenies) were evaluated in two experiments. The first experiment included F_1, F_2, and random mated generations for each of the four single crosses to evaluate the changes in the means. The second experiment included the

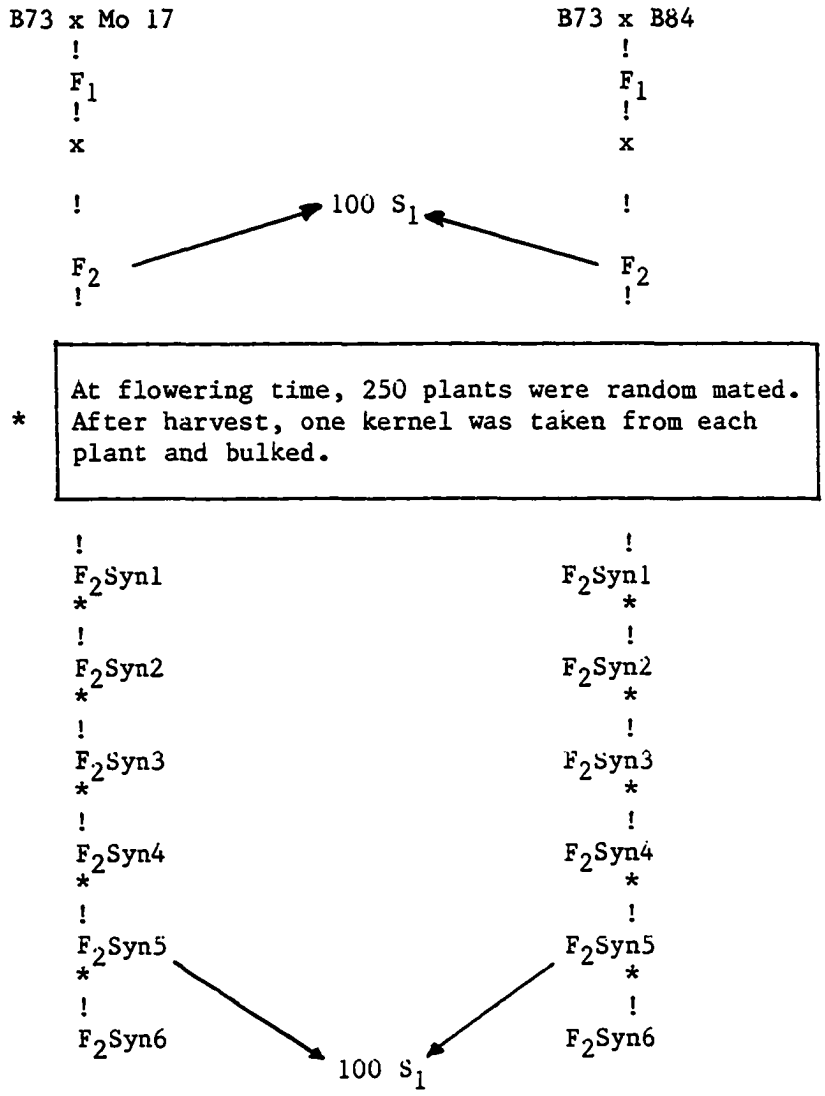

Figure 1. Methods used to develop the materials included to study changes in genetic variability with random mating

progenies derived from the F_2 and the F_2Syn5 generations of the B73 x Mo17 and B73 x B84 single crosses. Each generation was represented by 100 S_1 progenies.

Experiment 1

Three experiments were conducted at three locations during 1984 and 1985. The locations included Ames, Ankeny, and Martinsburg, Iowa. The experiment at Ames was located on the Agronomy and Agricultural Engineering Research Center.

Each experiment was planted in two-row plots that were 5.5 m long with 0.76 m between rows. The plots were overplanted using a machine planter. Approximately 25 days after emergence, the plots were thinned to 40 plants per plot. The plant density was approximately of 51,645 plants per hectare. All experiments were machine-harvested.

Data were collected for the following traits in each experiment:

1. STAND was recorded as the number of plants per plot. It was measured in each environment before flowering.

2. PERCENTAGE OF ROOT LODGING (PERTLG) was recorded before harvest as the number of plants per plot leaning 30° or more from the vertical. PERTLG was expressed as percentage of STAND.

3. PERCENTAGE OF STALK LODGING (PESTLG) was recorded before harvest as the number of plants per plot with stalks broken below or at the top ear node. PESTLG was expressed as percentage of STAND.

4. PERCENTAGE OF DROPPED EARS (PEDREA) was recorded as the number of ears on the ground at harvest. PEDREA was expressed as percentage

of STAND.

5. GRAIN YIELD (YIELD) was recorded as the shelled grain per plot and expressed in kilograms per plot.

6. MOISTURE CONTENT (MOIST) was determined at harvest from a sample obtained from the total shelled grain per plot. MOIST was expressed as percent and used to correct the field weight to get commercial weight.

Experiment 2

Two experiments were conducted at two locations in 1984 and 1985. Two locations were the Agronomy and Agricultural Engineering Research Center and Atomic Energy Research Center. Both locations are near Ames, but each location is environmentally different because of soil type and heat unit accumulation.

The materials evaluated in these experiments were the 400 S_1 progenies derived from the

(B73 x Mo 17) F_2,

(B73 x Mo 17) F_2Syn5,

(B73 x B84) F_2, and

(B73 x B84) F_2Syn5 populations. One hundred S_1 progenies were included for each population.

The plots used in these experiments included one row 5.5 m long with 0.76 m between plots. The plots were overplanted and thinned 15 days after emergence to give a final stand density of 51,645 plants per hectare. Experiments were hand harvested, and the ear corn was dried

at the Agronomy and Agricultural Engineering Research Center to a uniform moisture content of about 6%. Dried ear corn was shelled for yield determination.

Data were collected for the following traits in each environment:

1. STAND,

2. PERCENTAGE OF ROOT LODGING (PERTLG),

3. PERCENTAGE OF STALK LODGING (PESTLG),

4. PERCENTAGE OF DROPPED EARS (PEDREA), and

5. GRAIN YIELD (YIELD), expressed in kilograms per hectare.

Data for each of the traits were recorded in the same manner as described for the previous experiment.

6. DATE OF SILKING (DAYSIL) was recorded as the number of days after planting when at least 51% of the plants in a plot were showing silks. Data were recorded at both locations in 1985.

7. PLANT HEIGHT (PTAHE) was recorded in centimeters from the ground level to the flag leaf collar. It was measured for five competitive plants within each plot and was expressed on a plot mean basis.

8. EAR HEIGHT (EARHE) was recorded in centimeters from the ground level to the upper most ear bearing node. Five competitive plants were measured and ear height was expressed on a plot mean basis.

9. EAR LENGTH (EARLG) was recorded in centimeters as the total lenght of five randomly sampled ears from each plot and expressed as the mean of the five ears.

10. EAR DIAMETER (EARDIM) was recorded in centimeters as the total diameter of the same five randomly sampled ears measured for ear length

and expressed as the mean of the five ears.

11. COB DIAMETER (COBDIM) was recorded in centimeters as the total diameter of five randomly sampled ears and expressed as the mean of the five ears.

12. KERNEL DEPTH (KERDEP) was recorded in centimeters as half the difference between ear diameter and cob diameter of the ears measured for ear and cob diameter.

13. NUMBER OF KERNEL ROWS (ROWNO) was recorded as the average number of kernel rows for the five randomly sampled ears used for the ear measurements and expressed on a mean basis.

14. PROLIFICACY (PROLIF) was recorded as the relation of the number of ears produced in a plot to the STAND for that plot.

15. EAR INDEX (EARIND) was recorded as the relation of ear height to plant height for each plot.

Statistical Procedures

The experimental design used in the estimation of the generation means was a randomized complete block design with three replications for each experiment. Each experiment included 32 entries (Table 1).

An outline of the analysis of variance for a single experiment conducted in a specific environment and expected mean squares are presented in Table 2.

The statistical model used for the analysis of variance of the experiments conducted in one environment was the following linear additive model:

$$Y_{ij} = \mu + R_i + G_j + e_{ij},$$

where

Y_{ij} = observed value for the jth entry in the ith replication

(j=1,2,3, ... ,32; i=1,2,3);

Table 1. Materials used to evaluate the changes in means of four F_2 populations through six generations of random mating

Entry number	Entry	Entry number	Entry
1.	(B73 x Mo17) F_1	17.	(B73 x B79) F_1
2.	(B73 x Mo17) F_2	18.	(B73 x B79) F_2
3.	(B73 x Mo17) F_2Syn1	19.	(B73 x B79) F_2Syn1
4.	(B73 x Mo17) F_2Syn2	20.	(B73 x B79) F_2Syn2
5.	(B73 x Mo17) F_2Syn3	21.	(B73 x B79) F_2Syn3
6.	(B73 x Mo17) F_2Syn4	22.	(B73 x B79) F_2Syn4
7.	(B73 x Mo17) F_2Syn5	23.	(B73 x B79) F_2Syn5
8.	(B73 x Mo17) F_2Syn6	24.	(B73 x B79) F_2Syn6
9.	(B73 x B84) F_1	25.	(B77 x Mo17) F_1
10.	(B73 x B84) F_2	26.	(B77 x Mo17) F_2
11.	(B73 x B84) F_2Syn1	27.	(B77 x Mo17) F_2Syn1
12.	(B73 x B84) F_2Syn2	28.	(B77 x Mo17) F_2Syn2
13.	(B73 x B84) F_2Syn3	29.	(B77 x Mo17) F_2Syn3
14.	(B73 x B84) F_2Syn4	30.	(B77 x Mo17) F_2Syn4
15.	(B73 x B84) F_2Syn5	31.	(B77 x Mo17) F_2Syn5
16.	(B73 x B84) F_2Syn6	32.	(B77 x Mo17) F_2Syn6

μ = overall mean effect;

R_j = effect of the jth replication;

G_i = effect of the ith entry; and

e_{ij} = experimental error.

Table 2. Analysis of variance and expected mean squares for experiment conducted in one environment

Source of variation	Degrees of freedom[a]	Mean Squares	Expected mean squares
Replications (R)	r-1		
Entries (G)	g-1	M 2	$0^2 + r0^2_g$
Error (E)	(r-1)(g-1)	M 1	0^2.
Total	rg-1 .		

[a]r and g designate number of replications and entries, respectively.

An outline of the combined analysis of variance for the experiments conducted in different environments and expected mean squares are presented in Table 3.

The following model was used for the experiments repeated over environments:

$$Y_{ijk} = \mu + E_i + R_{ij} + G_k + (GE)_{ik} + e_{ijk},$$

where

Y_{ijk} = observed value for the kth entry in the jth replication in the ith environment (i=1,2, ... ,6; j=1,2,3; k=1,2,

... ,32);

μ = overall mean effect;

E_i = effect of the ith environment;

R_{ij} = effect of the jth replication within the ith environment;

G_k = effect of the kth entry;

$(GE)_{ik}$ = interaction effect of the kth entry with the ith environment; and

e_{ijk} = experimental error.

All variables except entries were considered as random effects in the linear model.

Table 3. Analysis of variance and expected mean squares for the analysis of variance combined over environments

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Environments (E)	e-1	M 5	$\sigma^2 + g\sigma^2 R/E + rp\sigma^2 E$
Replications/E	e(r-1)	M 4	$\sigma^2 + g\sigma^2 R/E$
Entries (G)	g-1	M 3	$\sigma^2 + r\sigma^2 ge + reK^2 g$
G x E	(g-1)(e-1)	M 2	$\sigma^2 + r\sigma^2 ge$
E r r o r	e(g-1)(r-1)	M 1	σ^2

[a]e, r, and g indicate the number of environments, replications and entries, respectively.

In the combined analysis, direct F tests were available for all sources of variation. The significance of environments was tested

against the Replication/E source of variation; the significance of G was tested against G x E, which was tested against the experimental error.

When a particular source of variation was found to be significant, comparisons among means were made. The significance of the difference between two means was tested by using Tukey's procedure presented by Steel and Torrie (1980):

$$W = q_{\alpha}(p, f_2)S_{\bar{x}},$$

where

q_{α} = value obtained from a tabulated table;

α = significance level;

p = number of entries in the experiment;

f_2 = error degrees of freedom; and

$S_{\bar{x}}$ = standard error of the mean.

The W value was used to judge the significance of each of the observed differences.

The estimation of the average change in the generation means due to the effect of random mating was made by fitting a linear regression model (Draper and Smith, 1966):

$$Y_{ij} = \mu + b_j X_i + e_{ij},$$

where

Y_{ij} = observed value for the jth population in the ith generation;

μ = mean of the base population;

b_j = linear regression coefficient for the jth population;

X_i = effect of any variable in the ith generation; and

e_{ij} = deviations from the regression line.

The standard error (S. E.) of the regression coefficient was computed using the formula presented by Draper and Smith (1966):

$$\text{S. E. } (b_i) = \sqrt{\frac{S^2}{[\Sigma_i (X_i - \bar{X})^2]}},$$

where

b_i = ith linear regresion coefficient;

S^2 = error mean square;

X_i = ith observed value for any variable analyzed; and

$\bar{X}$ = mean of that particular variable.

The significance of the regression coefficient was tested using t-test as follows (Steel and Torrie, 1980):

$$t = b_i / \text{S. E. } (b_i).$$

The calculated "t" was compared with tabular "t" at n-1 d.f., n being the number of generations being analyzed.

The experimental design used for the evaluation of the S_1 progenies was a lines-within-sets arranged in incomplete blocks with two replications. The 400 S_1 progenies included in each experiment were divided into 10 sets of 40 lines each; the 40 S_1 progenies within each set included 10 S_1 progenies from each of the four populations.

The outline of the analysis of variance for a single set evaluated in an individual environment and their respective expected mean squares are presented in Table 4. This analysis was performed using the linear additive model:

$$Y_{ij} = \mu + R_i + G_j + e_{ij},$$

where

Y_{ij} = observed value of the jth progeny in the ith replication (i=1,2; j=1,2, ... ,40);

μ = overall mean effect;

Table 4. Analysis of variance, degrees of freedom, and expected mean squares for one set evaluated in one experiment

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Replications	r-1		
Entries	g-1	M 2	$\sigma^2 + r\sigma^2 g$
(B73xMo17)F_2 (A1)	g1-1	M21	$\sigma^2 + r\sigma^2 g1$
(B73xMo17)F_2Syn5 (A2)	g2-1	M22	$\sigma^2 + r\sigma^2 g2$
(B73xB84)F_2 (B1)	g3-1	M23	$\sigma^2 + r\sigma^2 g3$
(B73xB84)F_2Syn5 (B2)	g4-1	M24	$\sigma^2 + r\sigma^2 g4$
A1 vs A2	1		
B1 vs B2	1		
A vs B	1		
E r r o r	(g-1)(r-1)	M 1	σ^2
Total	rg-1		

[a] r and g indicate number of replications and generations, respectively.

R_i = effect of the ith replication;

G_j = effect of the jth line; and

e_{ij} = experimental error.

In the models used in the analysis of the S_1 progenies, all effects were considered random.

The analysis of variance, pooled over sets, for each environment is outlined in Table 5 with expected mean squares. The statistical model for the analysis pooled over sets for one environment was the following linear additive model:

$$Yijk = \mu + S_i + R_{ij} + G_k + e_{ijk},$$

where

Y_{ijk} = observed value of the kth line within the ith set in the jth replication (i=1,2, ... ,10; j=1,2; k=1,2, ... 40);

μ = overall mean effect;

S_i = effect of the ith set;

R_{ij} = effect of the jth replication within the ith set;

G_{ik} = effect of the kth line within the ith set; and

e_{ijk} = experimental error.

Several analyses of variance were performed separately for each population (i.e., A1, A2, B1, B2) to obtain the partition due to lines/sets and pooled error in principal effects and their respective contrasts. For example, the contrast A1 vs A2 was obtained as: (A1 + A2) SS - (A1) SS - (A2) SS and divided by their respective degrees of freedom. The same procedure was repeated for each contrast within each source of variation. Another contrast was calculated, but it is not

Table 5. Analysis of variance pooled over sets for one environment

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Sets (S)	s-1		
Replications (R)/S	s(r-1)		
Progenies (G)/S	s(g-1)	M_2	$\sigma_1^2 + r\sigma_g^2$
(B73 x Mo17)F_2 (A1)	s(g1-1)	M_{21}	$\sigma_{11}^2 + r\sigma_{g1}^2$
(B73 x Mo17)F_2 Syn 5 (A2)	s(g2-1)	M_{22}	$\sigma_{12}^2 + r\sigma_{g2}^2$
(B73 x B84)F_2 (B1)	s(g3-1)	M_{23}	$\sigma_{13}^2 + r\sigma_{g3}^2$
(B73 x B84)F_2 Syn 5 (B2)	s(g4-1)	M_{24}	$\sigma_{14}^2 + r\sigma_{g4}^2$
A1 vs A2	(1)s		
B1 vs B2	(1)s		
A vs B	(1)s		
Pooled error	s(r-1)(g-1)	M_1	σ_1^2
(B73 x Mo17)F_2	s(r-1)(g1-1)	M_{11}	σ_{11}^2
(B73 x Mo17)F_2 Syn 5	s(r-1)(G2-1)	M_{12}	σ_{12}^2
(B73 x B84)F_2	s(r-1)(g3-1)	M_{13}	σ_{13}^2
(B73 x B84)F_2 Syn 5	s(r-1)(g4-1)	M_{14}	σ_{14}^2
A1 vs A2	s(1)(r-1)		
B1 vs B2	s(1)(r-1)		
A vs B	s(1)(r-1)		
Total	srg-1		

[a] s, r, and g indicate the number of sets, replications, and lines, respectively.

indicated in the tables, namely:

(A1+A2+B1+B2) SS - (A1+B1) SS - (A2+B2) SS

This contrast was used to compare the general effect of both F_2 vs F_2Syn5 in both populations.

All variables in these analyses were considered random.

Based on expected mean squares, appropriate F-tests were performed by the ratio of the larger component to the smaller component; the significance of this ratio was determined by comparison of calculated values with the tabulated values of the F-ratio with their corresponding degrees of freedom of both components. Each partition within lines/sets was tested against their respective pooled error partition.

$$F = \frac{M\,2_i}{M\,1_i} \quad \text{with d.f. } M2_i, \text{ d.f. } M1_i.$$

The analysis of variance pooled over sets and combined over environments is outlined in Table 6. The linear statistical model used to perform these analyses was:

$$Y_{ijkl} = \mu + E_i + S_j + (ES)_{ij} + (R/S/E)_{ijk} + (G/S)_{lk} + [(G/S)E]_{ijl} + e_{ijkl},$$

where

Y_{ijkl} = observed value of the lth line within the kth replication within the jth set in the ith environment;

μ = overall mean effect;

E_i = effect of the ith environment;

S_j = effect of the jth set;

$(ES)_{ij}$ = interaction effect between the jth set and the ith

Table 6. Analysis of variance, degrees of freedom, and expected mean squares pooled over sets and combined over environments

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Environments (E)	(e-1)		
Sets (S)	(s-1)		
G x S	(e-1)(s-1)		
Replications (R)/S/E	se(r-1)		
Progenies (G)/S	s(g-1)	M_3	$\sigma_1^2 + r\sigma_{ge}^2 + re\sigma_g^2$
(B73 x Mo17)F_2 (A1)	s(g1-1)	M_{31}	$\sigma_{11}^2 + r\sigma_{ge1}^2 + re\sigma_{g1}^2$
(B73 x Mo17)F_2 Syn 5 (A2)	s(g2-1)	M_{32}	$\sigma_{12}^2 + r\sigma_{ge2}^2 + re\sigma_{g2}^2$
(B73 x B84)F_2 (B1)	s(g3-1)	M_{33}	$\sigma_{13}^2 + r\sigma_{ge3}^2 + re\sigma_{g3}^2$
(B73 x B84)F_2 Syn 5 (B2)	s(g4-1)	M_{34}	$\sigma_{14}^2 + r\sigma_{ge4}^2 + re\sigma_{g4}^2$
A1 vs A2	s(1)		
B1 vs B2	s(1)		
A vs B	s(1)		

Progenies/Sets x E	s(g-1)(e-1)	M_2	$\sigma_1^2 + r\sigma_{ge}^2$
(B73 x Mo17)F_2 (A1)	s(g1-1)(e-1)	M_{21}	$\sigma_{11}^2 + r\sigma_{ge1}^2$
(B73 x Mo17)F_2 Syn 5 (A2)	s(g2-1)(e-1)	M_{22}	$\sigma_{12}^2 + r\sigma_{ge2}^2$
(B73 x B84)F_2 (B1)	s(g3-1)(e-1)	M_{23}	$\sigma_{13}^2 + r\sigma_{ge3}^2$
(B73 x B84)F_2 Syn 5 (B2)	s(g4-1)(e-1)	M_{24}	$\sigma_{14}^2 + r\sigma_{ge4}^2$
A1 vs A2	s(1)(e-1)		
B1 vs B2	s(1)(e-1)		
A vs B	s(1)(e-1)		
Pooled error	se(r-1)(g-1)	M_1	σ_1^2
A1	se(r-1)(g1-1)	M_{11}	σ_{11}^2
A2	se(r-1)(g2-1)	M_{12}	σ_{12}^2
B1	se(r-1)(g3-1)	M_{13}	σ_{13}^2
B2	se(r-1)(g4-1)	M_{14}	σ_{14}^2
A1 vs A2	se(1)(r-1)		
B1 vs B2	se(1)(r-1)		
A vs B	se(1)(r-1)		
Total	resg-1		

[a] e, s, r, and g indicate the number of environments, sets, replications, and progenies, respectively.

environment;

$(R/S/E)_{ijk}$ = effect of the kth replication within the jth set within the ith environment;

$(G/S)_{jl}$ = effect of the lth line within the jth set;

$[(G/S)E]_{ijl}$ = interaction effect between the lth line within the jth set and the ith environment; and

e_{ijkl} = pooled experimental error.

Direct F-tests were available for all sources of variation. Tests of significance of primary interest were those involving progenies within sets and the partitions of this source of variation. This source of variation was tested against its interaction effect with environments, which was tested against the pooled error. The same procedures indicated for the pooled analysis in one environment for the testing of significance of each partition within each source of variation [lines/sets and (lines/sets)*E] was followed.

Genetic variances were calculated for the individual and combined experiments. Estimates of the genetic variance components for each population were computed by equating observed mean squares to the expected mean squares. In individual experiments, estimates of genetic variances for each population were calculated from Table 5 as follows:

$\sigma^2_g = (M2 - M1)/r$ for total genetic variance;

$\sigma^2_{g_1} = (M21 - M11)/r$ for (B73 x Mo17)F_2;

$\sigma^2_{g_2} = (M22 - M12)/r$ for (B73 x Mo17)F_2Syn5;

$\sigma^2_{g_3} = (M23 - M13)/r$ for (B73 x B84)F_2; and

$\sigma^2_{g_4} = (M24 - M14)/r$ for (B73 x B84)F_2Syn5.

From the combined analysis, the estimates of genetic variances and the variances due to G x E interaction were computed as follows:

$\sigma^2 g_1 = (M31 - M21)/re$ for (B73 x Mo17)F_2 (A1);

$\sigma^2 g_2 = (M32 - M22)/re$ for (B73 x Mo17)F_2Syn5 (A2);

$\sigma^2 g_3 = (M33 - M23)/re$ for (B73 x B84)F_2 (B1);

$\sigma^2 g_4 = (M34 - M24)/re$ for (B73 x B84)F_2Syn5 (B2);

$\sigma^2 ge_1 = (M21 - M11)/r$ for A1;

$\sigma^2 ge_2 = (M22 - M12)/r$ for A2;

$\sigma^2 ge_3 = (M23 - M13)/r$ for B1; and

$\sigma^2 ge_4 = (M24 - M14)/r$ for B2.

Standard errors for the components of variance estimates to determine the precision of the estimates were computed by use of the formula (Anderson and Bancroft, 1952; Hallauer and Miranda, 1981):

$$S.E.(Var.) = \sqrt{\frac{2}{C^2} \frac{(MS_K)^2}{(DF_K + 2)}},$$

where

S.E. = standard error of any component;

C = coefficient preceding the variance components in the expected mean squares;

MS_K = kth mean squares involved in the estimation of the components of variance; and

DF_K = degrees of freedom associated with the kth mean square.

Variance components greater than twice their standard errors were judged to be significantly different from zero.

Estimates of heritability (h^2) on a progeny mean basis were calculated using the variance components estimates from the analysis of variance combined over environments by use of the formula (Falconer, 1981):

$$h^2 = \sigma^2 g / \sigma^2 ph,$$

where

$\sigma^2 g$ = genotypic variance among S_1 lines = $\sigma^2 A + 1/4\ \sigma^2 D$

($\sigma^2 A$, $\sigma^2 D$=additive and dominance genetic variance, respectively); and

$\sigma^2 ph$ = phenotypic variance = $\sigma^2 g + \sigma^2 ge/r + \sigma^2/re$, where

$\sigma^2 ge$ = genotype x environment interaction variance;

σ^2 = experimental error; and

r, e = the number of replications and environments, respectively.

The expression used to measure the precision of h^2 is $h^2 \pm SE(h^2)$, but this distribution is misrepresented because the F-distribution is left skewed (Knapp et al., 1985); therefore, the accurate measure of precision for h^2 estimates used in this study was the confidence intervals proposed by Knapp et al. (1985) as follows:

$$P\{1 - [(M1/M2)F_{1-\alpha/2;\ df2,\ df1}]^{-1} < h^2 < 1 - [(M1/M2)F_{\alpha/2;\ df2,\ df1}]^{-1}\} = 1 - \alpha;$$

where

$1 - \alpha$ = probability level;

M1 = mean square for progenies/set;

M2 = mean square for progenies/set * E;

df1, df2 = degrees of freedom for M1 and M2, respectively; and

$F_{df1,\ df2}$ = values from this distribution at 0.05 level that were obtained by interpolation (Hald, 1952) as

$$F_{df1,\ df2} = \log_{10} F_{.975} - 1.7023(h-1.14)^{-1} - 0.846(f1 - f2)^{-1},$$

where

$h^{-1} = [2\ (f1 + f2)]^{-1}$; and

$F_{df2,\ df1} = [F_{df1,\ df2}]^{-1}$.

Phenotypic correlation coefficients (r_p) were computed for the F_2 and F_2Syn5 in both single crosses (B73 x Mo17 and B73 x B84) by use of the formula (Mode and Robinson, 1959):

$$r_p = \sigma_{pxy}\ (\sigma^2 px * \sigma^2 py)^{-1/2},$$

where

σ_{pxy} = phenotypic covariance between traits x and y;

$\sigma^2 px$ = phenotypic variance of trait x; and

$\sigma^2 py$ = phenotypic variance of trait y.

r_p measures the real phenotypic correlation only in the absence of epistasis; in the presence of epistasis, the above ratio will estimate some modified form of r_p, because σ_{pxy}, $\sigma^2 px$, and $\sigma^2 py$ will contain a fraction of the total phenotypic variance (Mode and Robinson, 1959).

The significance of the phenotypic correlations was tested by use of t-tests as follows (Steel and Torrie, 1980):

$$t = r_p\ [(1 - r^2)(n - 2)^{-1}]^{-1/2},$$

where

n = number of entries.

The significance of calculated t was estimated by using a tabulated t at n-2 degrees of freedom.

Genotypic correlation coefficients (r_g) were computed for the F_2 and F_2Syn5 in both single crosses (B73 x Mo17 and B73 x B84) by use of the formula (Mode and Robinson, 1959):

$$r_g = \delta_{Gxy} \, (\delta^2_{Gx} * \delta^2_{Gy})^{-1/2},$$

where

δ_{Gxy} = genotypic covariance between traits x and y;

δ^2_{Gx} = genotypic variance of trait x; and

δ^2_{Gy} = genotypic variance of trait y.

Phenotypic and genotypic correlations were estimated from the analysis of variance combined over environments by use of the MANOVA statement from SAS. The E and H matrices from the output were used to estimate both phenotypic and genotypic correlations by use of a program that is outlined in the Appendix.

The significance of the difference between the correlation coefficients between the F_2 and the F_2Syn5 were tested according to the formula presented by Steel and Torrie (1980); the two coefficients (r) are converted to Z' values and an appropriate large sample normal test is applied. The test includes the calculation of a Z value and compare that value with a standard normal distribution for the significance of the difference, as follows:

$$Z = \frac{Z'1 - Z'2}{\sqrt{n_i - 3}},$$

where

Z' = values of the converted correlation coefficients that are equal to 0.5 ln (1+r)/(1−r),

n = sample size, and

r = correlation coefficient.

RESULTS

Experiment 1

Effects of random mating on means

The results of the analysis of variance combined for the six environments are presented in Table 7. All F-tests for the different traits were made according to the expected mean squares (Table 3). Differences for each source of variation were statistically significant for all traits except the interaction of entries with environments for PERTLG. Significance for STAND was due to differences among the four single crosses for the generations of random mating; that is, those differences were not at random. The combined analyses were effective in removing variation due to REP/ENV, since most of the traits were significant for this source of variation.

The coefficients of variation (C.V.) for YIELD and MOIST were acceptable and within the range generally experienced for machine-harvested plots. The C.V.s for PERTLG, PESTLG, and PEDREA were higher because the percentages of lodging were relatively low, and their occurrences among locations were not consistent. There also were significant differences among environments for all traits, and the entries were not consistent across environments (Table 7). Some entries tended to show higher values for each trait in favorable environments and not in others. Entry performance for each environment is presented in Tables A1 and A2 in the Appendix. Entries were statistically significant

Table 7. Combined analysis of variance, means and coefficients of variation (C.V.) for six traits measured in six environments

Source of variation	df	Mean squares					
				Lodging		Grain moisture	Dropped ears
		Yield	Stand	Root	Stalk		
		kg plot^{-1}	plants plot^{-1}	%			
Environments (E)	5	283.83**	949.94**	7181.01**	5921.68**	152.96**	78.20**
Replications/E	12	9.61**	20.24*	82.92**	53.07^{ns}	5.57**	9.14**
Entries (G)	31	113.79**	69.68**	312.50*	353.71**	10.30**	8.29*
G x E	155	2.92**	11.85*	184.56**	78.14**	3.36**	4.67^{ns}
Error	372	2.06	9.17	30.82	47.05	2.25	3.80
Mean		10.55	44.87	5.55	12.27	22.06	1.46
C.V. (%)		13.60	6.75	100.01	55.93	6.80	133.38

*,**Indicates significance at 0.05 and 0.01 statistical levels, respectively.

^{ns}Indicates nonsignificance.

in some environments, and the variation among means for PERTLG, PESTLG, and PEDREA was large.

The analyses of variance for each environment are shown in Tables A1 and A2 in the Appendix. In 1984, the highest yields were registered at Ankeny, but with high C.V. (15.7%). In 1985, the lowest yield was registered at Ankeny with the highest C.V. because this location had to be replanted three weeks later, and this delay had a dramatic effect on yield (Hallauer et al., 1985). The location with lower yields in both years (1984 and 1985) was Martinsburg.

STAND had statistical significance among entries in three environments, while the other three trials showed no significant differences among entries. The differences among entries for stand were not consistent among environments (Table 7). PEDREA was statistically significant among entries only at Ankeny in 1984 and at Ames in 1985, and there was no significance of the interaction with environments in the combined analyses.

The differences in mean yield between years and among locations can be attributed to the erratic distribution and total amount of rainfall and the variation in temperatures (accumulated degree days). Hallauer et al. (1984,1985) presented meteorological data which indicate that the accumulated effective degree days in 1984 were below the average for the period 1976-84; the yields were low because of warm and dry conditions during August. The growing season in 1984 was extreme because it was too wet in early spring and too hot and dry in August and September. Growing conditions for corn production in 1985 tended

to be below normal for rainfall, but the temperatures were cool.

PERTLG was always less frequent than PESTLG. The exception was at Martinsburg where both traits had the same mean in 1985, but PERTLG was extremely high in 1984 because a tornado hit the experiment on July 14 and caused excessive PERTLG. Fortunately, the plants continued to grow to maturity due to an adequate moisture supply at grain filling stages (Hallauer et al., 1984). PESTLG was also high at Ankeny in 1985 due to very poor plant development and growth because of the delay in planting; another cause was the higher infestation by the European corn borer (Hallauer et al., 1984).

The mean values for six traits in each single cross by generation are included in Table 8. B73xMo17 showed the highest inbreeding depression from the F_1 to the F_2 and B73xB84 the lowest; this performance was expected because the parents in B73xMo17 are unrelated and showed high heterosis, while those in B73xB84 are related. The other two single crosses (B73xB79 and B77xMo17) showed inbreeding depressions that were intermediate between B73xMo17 and B73xB84.

The STAND was similar among generations for each single cross. Hence, the differences in yield were not due to differences in stand.

B77xMo17 had the lowest PERTLG among generations of random mating, suggesting B77xMo17 had greater resistance to root lodging. For B73xB79, the six generations of random mating were superior in PERTLG to the F_2 and F_1 generations.

The linear regression coefficients estimated for YIELD and MOIST for the four single crosses are included in Table 9. Regression coef-

Table 8. Mean values for six traits measured in the combined analysis of eight generations for four single crosses evaluated in six environments

Generations	Traits					
	Grain yield	Stand	Lodging		Grain moisture	Dropped ears
			Root	Stalk		
	kg plot^{-1}	plants plot^{-1}	----------		%----------	
B73 x Mo17						
F_1	19.4	49.1	7.2	4.6	21.8	1.0
F_2	10.1	46.8	9.4	7.5	22.2	2.0
F_2 Syn 1	10.7	45.6	8.2	9.6	20.9	1.9
F_2 Syn 2	10.3	39.9	7.9	8.6	20.8	1.1
F_2 Syn 3	10.7	45.2	6.0	11.2	20.8	3.2
F_2 Syn 4	10.4	43.2	11.9	9.1	21.2	2.3
F_2 Syn 5	10.7	43.7	6.6	6.0	20.5	1.1
F_2 Syn 6	10.9	45.1	7.6	7.4	20.6	2.5
B73 x B84						
F_1	13.9	44.1	10.4	7.1	22.7	1.0
F_2	11.3	46.4	9.0	9.5	22.9	2.0
F_2 Syn 1	10.4	45.2	10.4	11.4	21.9	1.9
F_2 Syn 2	10.8	44.7	7.0	8.1	22.6	1.1
F_2 Syn 3	10.0	39.8	9.1	10.1	22.5	3.2
F_2 Syn 4	10.8	45.8	8.4	8.8	21.9	2.3
F_2 Syn 5	10.9	43.3	8.8	12.4	22.0	1.1
F_2 Syn 6	11.2	46.4	9.2	11.1	21.8	2.5
B73 x B79						
F_1	16.0	45.9	12.4	11.6	22.8	0.3
F_2	10.5	47.1	11.6	10.8	23.4	0.5
F_2 Syn 1	8.3	43.1	1.5	14.5	23.0	2.0
F_2 Syn 2	8.9	46.3	0.4	22.0	22.6	1.3
F_2 Syn 3	8.5	44.1	2.9	14.9	22.7	1.8
F_2 Syn 4	8.1	44.2	0.8	17.4	22.6	1.9
F_2 Syn 5	8.4	43.7	1.4	18.4	22.2	2.5
F_2 Syn 6	8.9	43.7	1.1	18.6	22.2	1.2
B77 x Mo17						
F_1	16.0	47.4	0.6	8.0	22.8	1.9
F_2	9.5	47.1	0.8	16.9	22.0	1.4
F_2 Syn 1	8.6	42.6	1.0	14.6	22.4	1.5
F_2 Syn 2	8.4	46.1	1.0	15.5	22.6	2.4
F_2 Syn 3	8.8	45.0	0.1	19.1	22.0	1.4
F_2 Syn 4	9.0	45.4	1.4	14.2	22.1	1.8
F_2 Syn 5	8.4	44.6	2.5	15.5	21.6	1.6
F_2 Syn 6	9.0	45.3	1.1	18.1	21.7	1.2

Table 8. (Continued)

Generations	Traits					
	Grain yield	Stand	Lodging		Grain moisture	Dropped ears
			Root	Stalk		
	kg plot^{-1}	plants plot^{-1}	----------		%	----------
L.S.D.	0.9	2.0	3.7	4.5	1.0	1.3
H.S.D.	1.7	3.6	6.7	8.1	1.8	2.3

ficients for YIELD were not statistically different from zero for any of the four single crosses. The regression coefficients were positive for B73xMo17 and B73xB84 and negative for B73xB79 and B77xMo17. Re-

Table 9. Linear regression coefficients estimated for the F_2 and six generations of random mating in four single crosses evaluated in six environments

	Single crosses	
Traits	B73 x Mo17	B73 x B84
YIELD	$0.088 + 0.097^{ns}$	$0.021 + 0.09^{ns}$
MOIST	$-0.0019 + 0.0007^{*}$	$-0.0013 + 0.001^{ns}$
	B73 x B79	B77 x Mo17
YIELD	$-0.182 + 0.097^{ns}$	$-0.044 + 0.097^{ns}$
MOIST	$-0.002 + 0.0009^{*}$	$-0.0011 + 0.0008^{ns}$

*Indicates significance at 0.05 probability level.

nsIndicates nonsignificance.

gression coefficients for MOIST were negative and statistically different from zero for B73xMo17 and B73xB79.

Means (observed and predicted) for YIELD and MOIST of the F_2 and six generations of random mating are plotted for each single cross in Figures 2 to 9. The trend of generations of random mating in B73xMo17 is shown in Figure 2. The increase in yield of about 1% per generation was not significant. B73xB84 also had a nonsignificantly positive regression coefficient and no generation of random mating exceeded

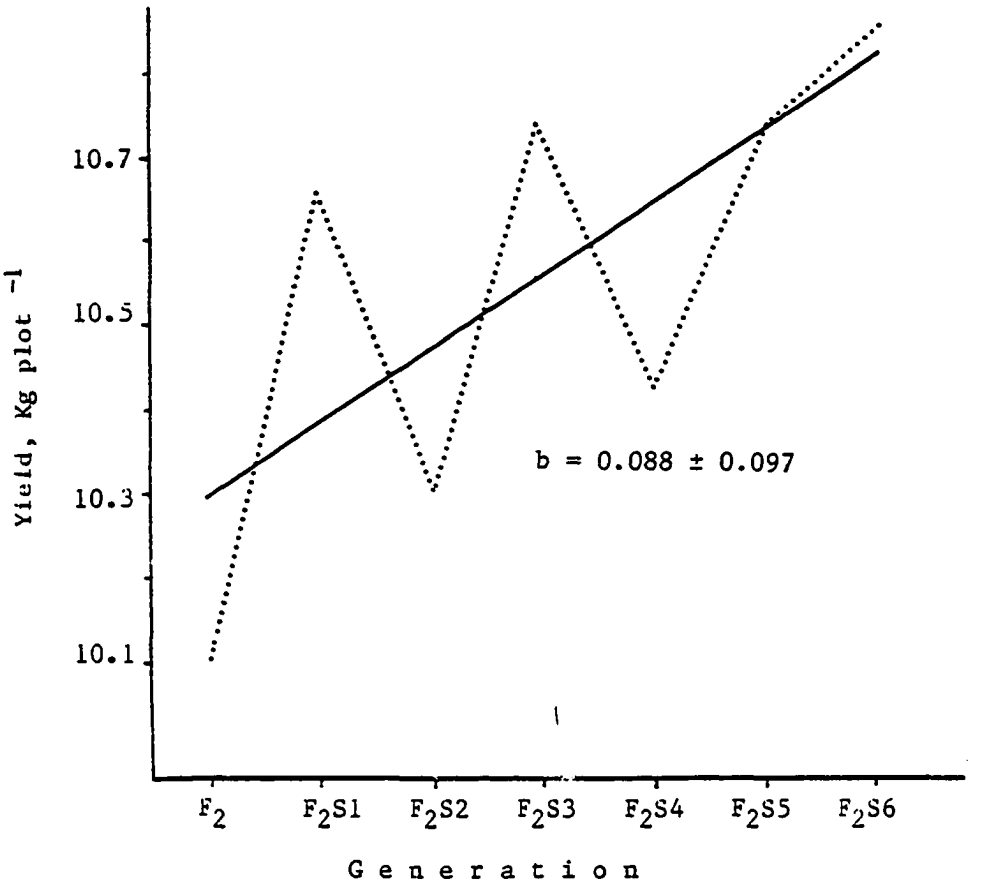

Figure 2. Observed (...) and fitted (___) grain yield means for the F_2 and six generations of random mating in B73xMo17 evaluated in six environments

the F_2 yield (Figure 3). The F_2 in B73xB84 was greater yielding than the F_2 in B73xMo17.

The trends for YIELD in B73xB79 and B77xMo17 were negative, and they were not statistically different from zero. The decrease in yield in B73xB79 was about 1.95% per generation of random mating; this coefficient was statistically significant at 0.07 probability level.

The best agreement between predicted and observed values for MOIST was observed in B73xB79. Significant decreases in MOIST were observed in B73xMo17 and B73xB79, which decreased 0.88% and 0.85% per generation, respectively. Therefore, there was a trend over the generations of random mating in B73xMo17 towards higher (but not significant) values of yield, coupled with a trend towards less (and significant) grain moisture content.

Experiment 2

The analyses of variance pooled over sets and combined over environments are presented in Table 10 for 14 traits. There were statistical differences among the S_1 progenies for the 14 traits measured. The interactions of S_1 progenies with environments were significantly different for all traits, except for EARHE, COBDIM, and EARDIM. As in the first experiment, PERTLG, PESTLG, and PEDREA had high C.V.s due to the relatively low means and greater errors in measurement. The C.V.s for all traits were within acceptable ranges, suggesting the data are reliable.

The differences observed among sets for PROLIF and ROWNO can be

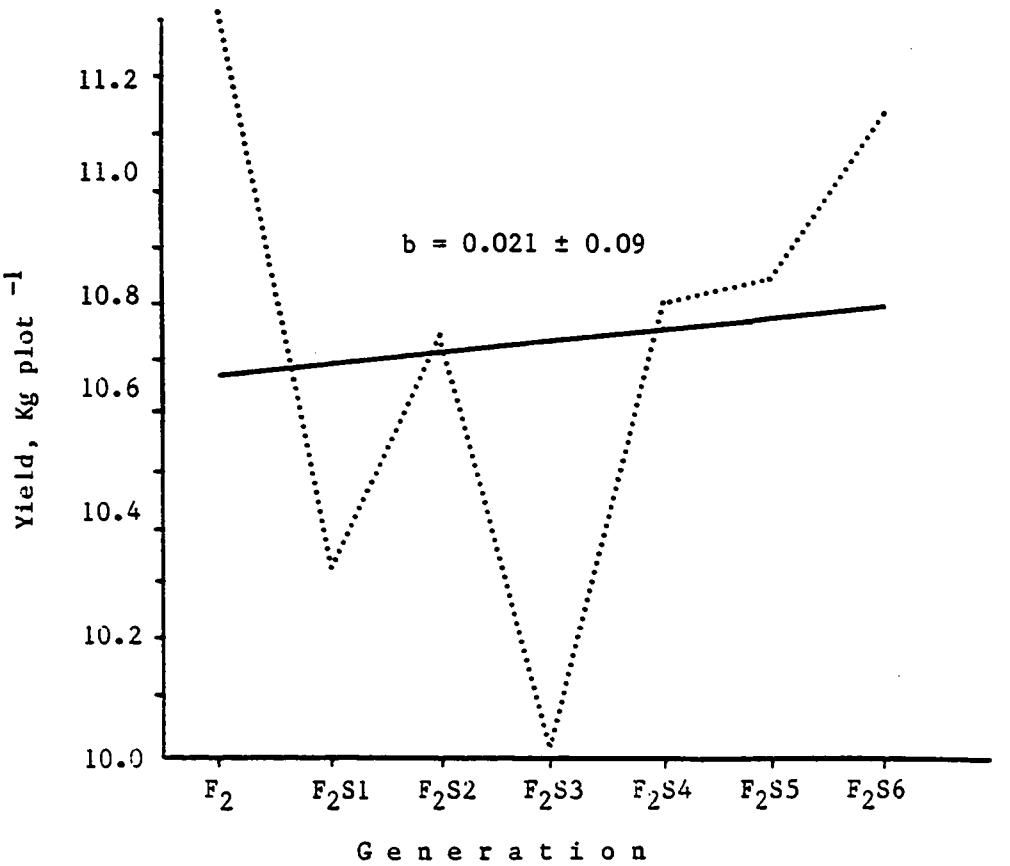

Figure 3. Observed (...) and fitted (___) grain yield means for the F_2 and six generations of random mating in B73xB84 evauated in six environments

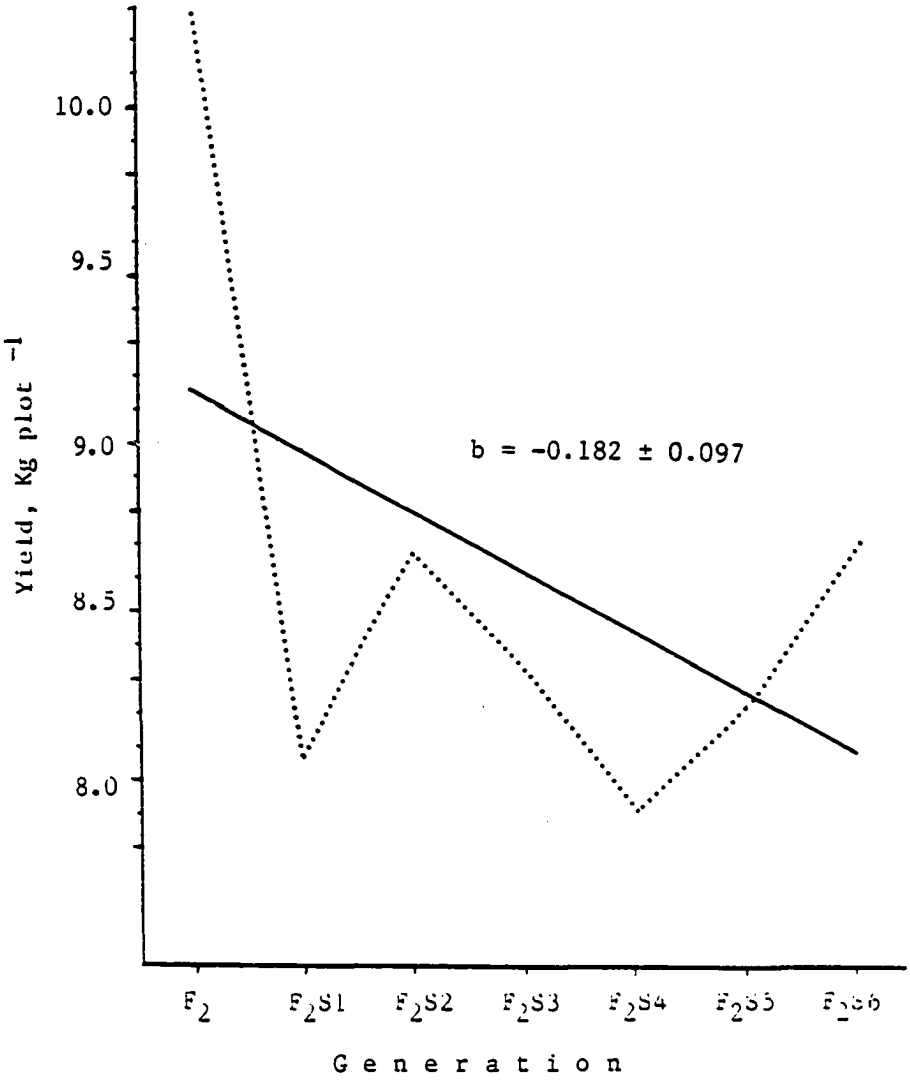

Figure 4. Observed (...) and fitted (___) grain yield means for the F_2 and six generations of random mating in B73xB79 evaluated in six environments

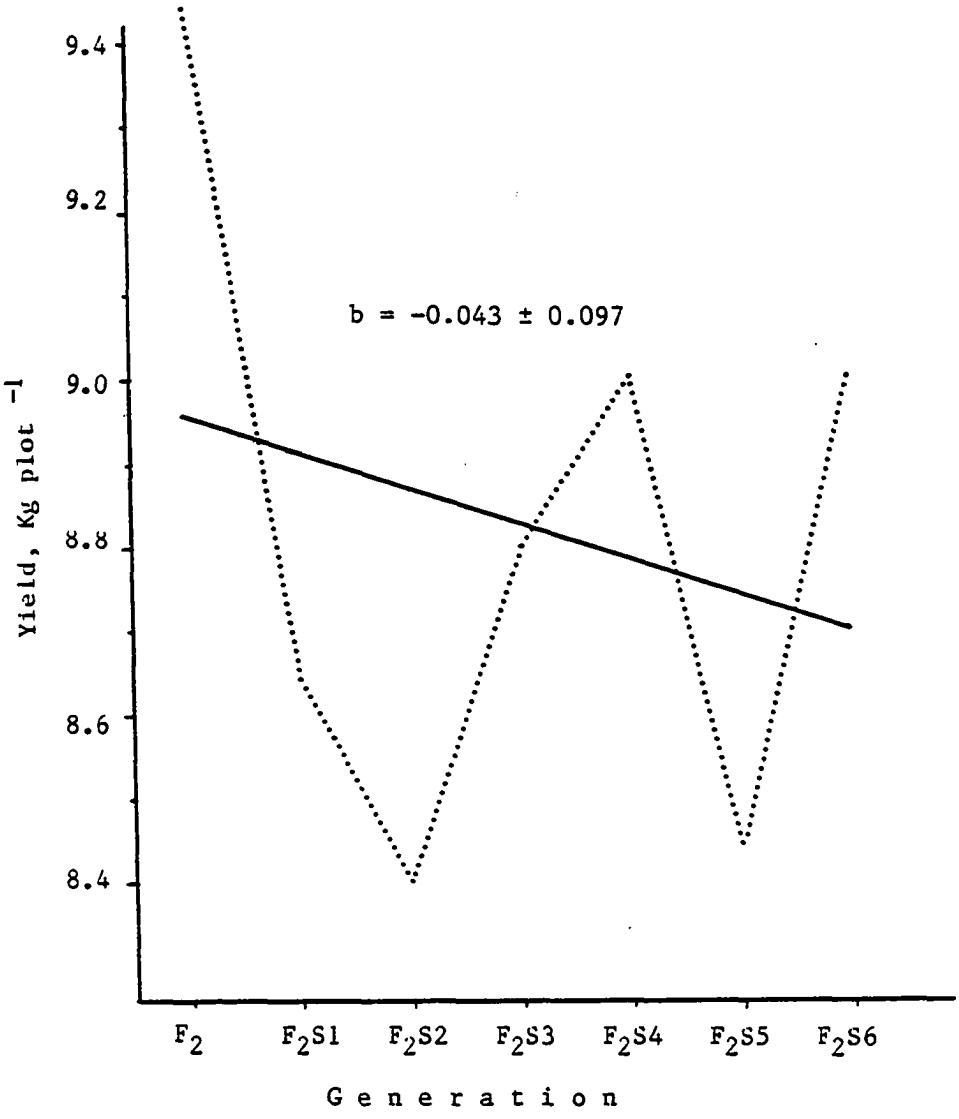

Figure 5. Observed (...) and fitted (___) grain yield means for the F_2 and six generations of random mating in B77xMo17 evaluated in six environments

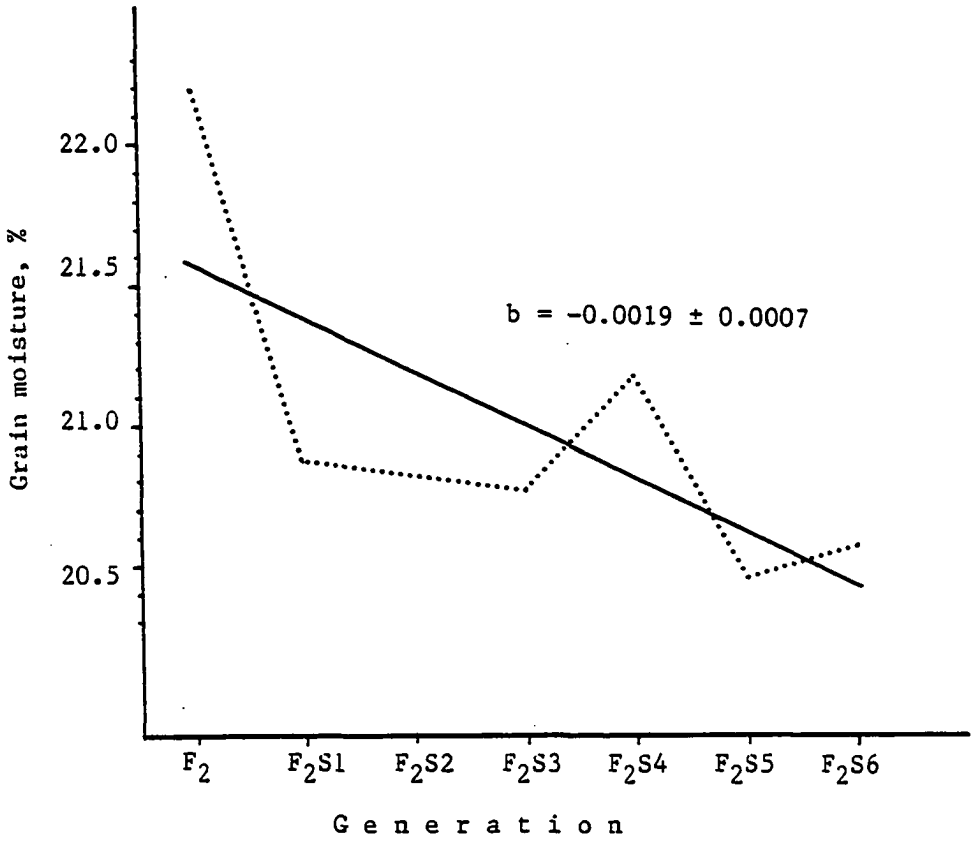

Figure 6. Observed (...) and fitted (___) grain moisture means for the F_2 and six generations of random mating in B73xM017 evaluated in six environments

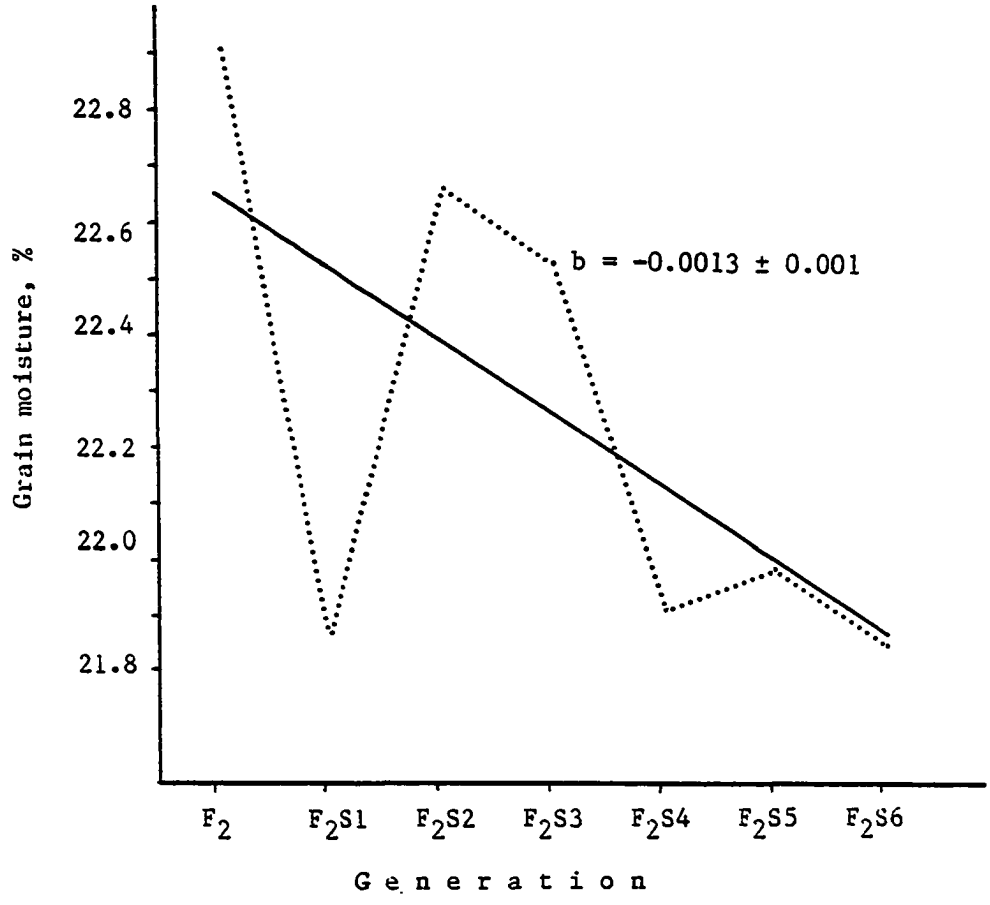

Figure 7. Observed (...) and fitted (___) grain moisture means for the F_2 and six generations of random mating in B73xB84 evaluated in six environments

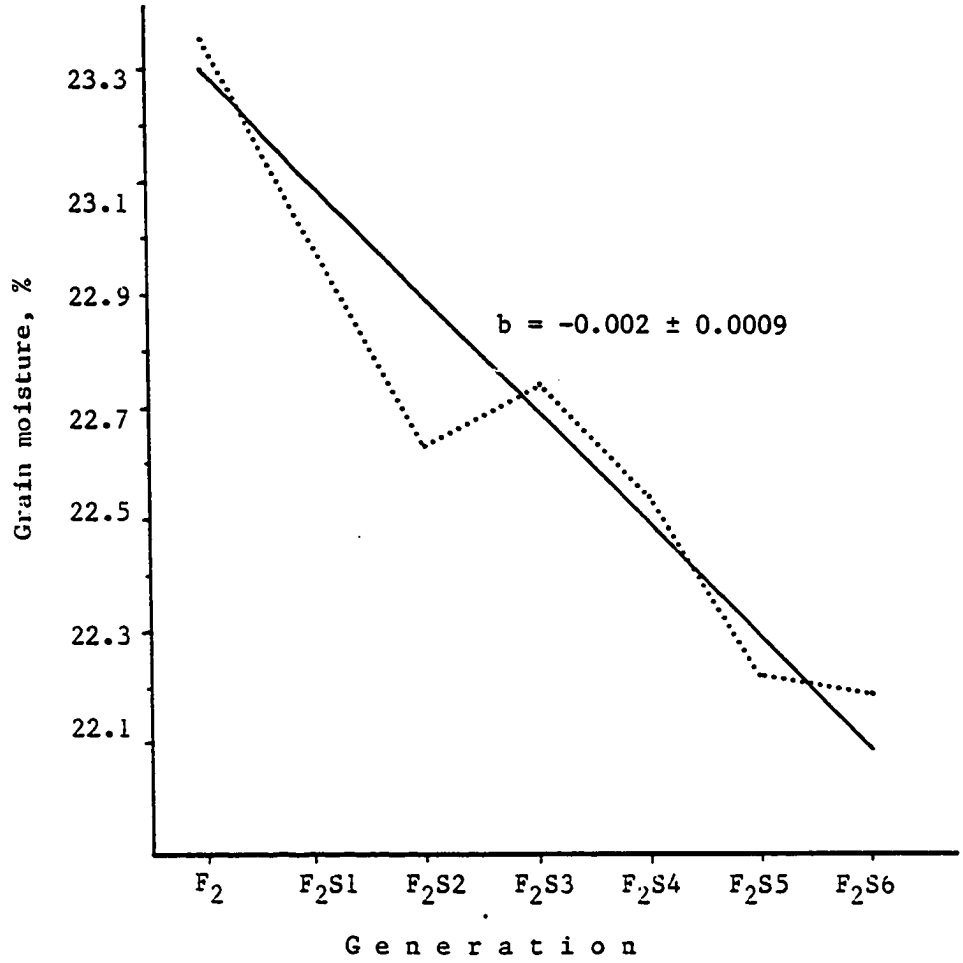

Figure 8. Observed (···) and fitted (___) grain moisture means for the F_2 and six generations of random mating in B73xB79 evaluated in six environments

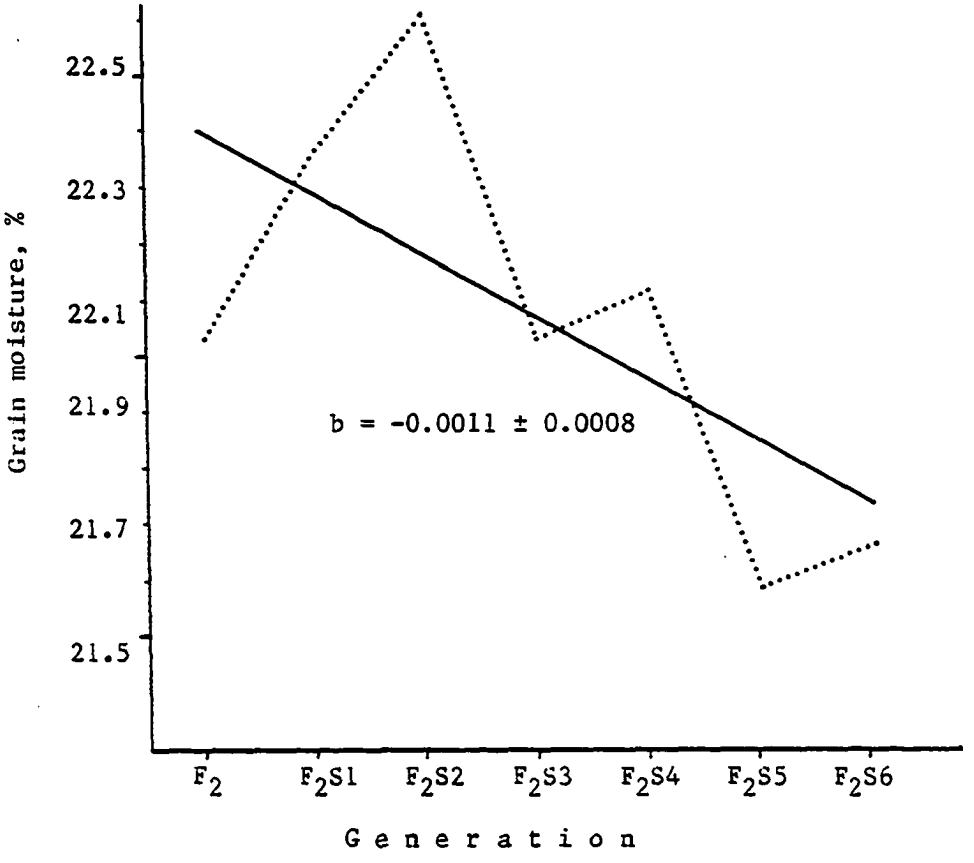

Figure 9. Observed (...) and fitted (___) grain moisture means for the F_2 and six generations of random mating in B77xMo17 evaluated in six environments

Table 10. Analysis of variance combined over environments, means, C.V., and partition of sums of squares for main sources for 14 traits evaluated in four environments at Ames (1984, 1985)

Source	df	Mean squares		
		Root lodging	Stalk lodging	Dropped ears
		----------%----------		
Environments (E)	3	11591.56**	11378.17**	158.93**
Sets (S)	9	621.00^{ns}	581.20^{ns}	4.37^{ns}
E x S	27	329.70**	392.47**	4.93**
Replications/S/E	40	45.89^{ns}	87.42**	3.42^{ns}
Progenies/S	390	159.18**	271.29**	5.02**
(B73 x Mo17)F_2	90	91.81**	338.42**	8.36**
(B73 x Mo17)F_2 Syn 5	90	66.88**	417.20**	5.48^{ns}
(B73 x B84)F_2	90	199.64**	80.63*	2.38**
(B73 x B84)F_2 Syn 5	90	205.00**	193.86**	1.54^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	10	83.11**	174.36^{ns}	5.32^{ns}
(B73 x B84)F_2 vs F_2 Syn 5	10	121.22^{ns}	185.11*	1.63^{ns}
(B73 x Mo17) vs (B73 x B84)	10	933.63**	949.91**	28.85*
Progenies/S x E	1170	89.09**	94.28**	3.68**
(B73 x Mo17)F_2	270	49.28^{ns}	112.17**	5.45**
(B73 x Mo17)F_2 Syn 5	270	42.30^{ns}	122.51**	5.78**
(B73 x B84)F_2	270	133.22**	56.89*	1.41^{ns}
(B73 x B84)F_2 Syn 5	270	107.96**	65.47**	1.37^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	30	48.67^{ns}	110.87**	4.37**
(B73 x B84)F_2 vs F_2 Syn 5	30	85.41**	82.01**	1.23^{ns}
(B73 x Mo17) vs (B73 x B84)	30	345.54**	270.71**	11.89**
Pooled error	1560	43.14	44.70	2.52
(B73 x Mo17)F_2	360	24.34	51.64	2.93
(B73 x Mo17)F_2 Syn 5	360	16.73	45.93	4.47
(B73 x B84)F_2	360	61.07	32.12	1.02
(B73 x B84)F_2 Syn 5	360	71.97	47.36	1.60
(B73 x Mo17)F_2 vs F_2 Syn 5	40	13.05	52.73	2.11
(B73 x B84)F_2 vs F_2 Syn 5	40	46.12	36.09	1.20
(B73 x Mo17) vs (B73 x B84)	40	56.47	61.10	5.02
$\bar{X}$		3.50	6.41	0.49
C.V.		187.8	104.3	326.8

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Mean squares					
Plant height	Ear height	Ear length	Ear diameter	Cob diameter	Ear index
cm					$(\frac{\text{Ear height}}{\text{Plant height}})$
185304.31**	22475.51**	319.96**	5.810**	2.540**	0.456**
1348.80^{ns}	412.75^{ns}	3.97^{ns}	0.218^{ns}	0.140^{ns}	0.011^{ns}
1624.09**	454.03**	6.68**	0.203**	0.083**	0.007**
150.63**	92.45**	2.13**	0.043**	0.016^{ns}	0.001**
1472.21**	755.20**	14.83**	0.198**	0.150**	0.008**
1439.80**	827.26**	7.91**	0.304**	0.128**	0.0058**
1422.55**	958.78**	6.98**	0.209**	0.071**	0.0093**
771.86**	443.10**	6.11**	0.108**	0.077**	0.0043**
775.26**	490.45**	8.59**	0.146**	0.070**	0.0056**
3420.80**	2547.31**	18.25**	0.176**	0.097**	0.0148**
5153.37**	1858.52**	7.25**	0.211**	0.035**	0.0041**
9156.58**	570.66**	286.62**	0.412**	2.62**	0.0673**
88.49*	44.36^{ns}	1.25**	0.029*	0.017^{ns}	0.0006^{ns}
79.58^{ns}	44.72^{ns}	1.56**	0.027^{ns}	0.016^{ns}	0.0006^{ns}
73.57^{ns}	45.94^{ns}	1.50**	0.032**	0.017^{ns}	0.0007**
74.84^{ns}	38.23^{ns}	0.92^{ns}	0.023^{ns}	0.017^{ns}	0.0006^{ns}
80.62^{ns}	36.63^{ns}	0.91^{ns}	0.023^{ns}	0.017^{ns}	0.0006^{ns}
112.60*	71.63**	1.85**	0.043**	0.017^{ns}	0.0008**
90.71^{ns}	42.46^{ns}	0.62^{ns}	0.018^{ns}	0.015^{ns}	0.0006^{ns}
470.47**	126.42**	2.43**	0.122**	0.019^{ns}	0.0007^{ns}
66.84	37.78	0.89	0.022	0.014	0.0005
68.23	43.96	1.06	0.022	0.0137	0.00052
58.00	37.38	0.98	0.025	0.0143	0.00054
74.11	37.98	0.74	0.021	0.0130	0.00056
63.75	31.42	0.77	0.020	0.0142	0.00049
69.78	49.81	0.96	0.026	0.0208	0.00064
87.26	31.12	0.95	0.018	0.0173	0.00049
72.73	35.70	0.79	0.018	0.0213	0.00039
185.94	92.59	14.96	4.38	2.71	0.50
4.42	6.64	6.32	3.37	4.41	4.58

Table 10. (Continued)

Source	df	Mean squares	
		Prolificacy	Kernel depth
		no.	cm
Environments (E)	3	0.483**	2.74**
Sets (S)	9	0.127*	0.027^{ns}
E x S	27	0.050**	0.021**
Replications/S/E	40	0.018*	0.0115*
Progenies/S	390	0.112**	0.0376**
(B73 x Mo17)F_2	90	0.076**	0.0336**
(B73 x Mo17)F_2 Syn 5	90	0.143**	0.0319**
(B73 x B84)F_2	90	0.045**	0.0184**
(B73 x B84)F_2 Syn 5	90	0.066**	0.0257**
(B73 x Mo17)F_2 vs F_2 Syn 5	10	0.173**	0.0260**
(B73 x B84)F_2 vs F_2 Syn 5	10	0.066**	0.0350**
(B73 x Mo17) vs (B73 x B84)	10	1.154**	0.4210**
Progenies/S x E	1170	0.017**	0.0081*
(B73 x Mo17)F_2	270	0.011^{ns}	0.0077^{ns}
(B73 x Mo17)F_2 Syn 5	270	0.016*	0.0076^{ns}
(B73 x B84)F_2	270	0.017**	0.0077^{ns}
(B73 x B84)F_2 Syn 5	270	0.019**	0.0073^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	30	0.021**	0.0093^{ns}
(B73 x B84)F_2 vs F_2 Syn 5	30	0.013^{ns}	0.0063^{ns}
(B73 x Mo17) vs (B73 x B84)	30	0.044**	0.0272**
Pooled error	1560	0.012	0.0068
(B73 x Mo17)F_2	360	0.0107	0.0072
(B73 x Mo17)F_2 Syn 5	360	0.0137	0.0065
(B73 x B84)F_2	360	0.0107	0.0071
(B73 x B84)F_2 Syn 5	360	0.0132	0.0067
(B73 x Mo17)F_2 vs F_2 Syn 5	40	0.0123	0.0063
(B73 x B84)F_2 vs F_2 Syn 5	40	0.0091	0.0047
(B73 x Mo17) vs (B73 x B84)	40	0.0169	0.0057
$\bar{X}$		0.98	0.83
C.V.		11.26	9.89

Mean squares			
Row number	Grain yield	df	Days to silking
cm	$(kg\ ha^{-1})^{-3}$		no.
143.52**	556939.37**	1	906.01**
11.05**	2110.87^{ns}	9	34.59^{ns}
2.24**	2431.31**	9	18.95**
0.45^{ns}	1467.55**	20	4.78**
16.39**	4298.68**	390	21.91**
11.77**	5801.06**	90	24.85**
7.13**	5240.48**	90	18.20**
12.08**	2447.08**	90	11.06**
10.33**	3370.73**	90	13.29**
10.65**	8887.60**	10	46.42**
14.98**	1507.41*	10	5.37^{ns}
241.94**	5519.39*	10	196.27**
0.75*	781.04**	390	2.38**
0.66^{ns}	650.65**	90	2.24^{ns}
0.72^{ns}	1030.80**	90	2.49^{ns}
0.70^{ns}	635.18**	90	2.18^{ns}
0.80*	633.39**	90	2.30^{ns}
0.73^{ns}	1308.32**	10	4.03**
0.98*	634.78^{ns}	10	1.90^{ns}
1.62**	1967.19**	10	4.20^{ns}
0.63	440.33	780	1.76
0.5169	502.78	180	1.64
0.6413	518.39	180	2.04
0.6648	361.44	180	1.64
0.6573	352.68	180	1.83
0.4728	489.94	20	0.81
0.9267	372.31	20	0.86
0.7058	692.85	20	2.76
15.94	4688.99		85.37
4.96	14.15		1.56

attributed to the environment because each set was composed of random lines. The arrangement of REP/SET was effective in removing some of the environmental variation. Except for COBDIM, ROWNO, PERTLG, and PEDREA, the REP/SET was statistically significant.

Significant differences were detected among S_1 progenies in the F_2 and in the F_2Syn5 in both single crosses. The contrast B73xMo17 VS B73xB84 was statistically different for all 14 traits measured; this result was expected due to the relationship among the inbreds included in each cross. The contrast F_2 VS F_2Syn5 in B73xMo17 was significantly different for all traits except for PESTLG and PEDREA, suggesting that changes have occurred among the generations of random mating. These contrasts show that means of the two populations, averaged over environments, were different in at least one environment. The contrast F_2 VS F_2Syn5 in B73xB84 did not show statistical differences for DAYSIL, PERTLG, and PEDREA. The F_2 and F_2Syn5 generations in both single crosses had similar performance for PEDREA; therefore, the means for the F_2 and the F_2Syn5 for each single cross were similar.

Comparisons between the F_2 and F_2Syn5 generations pooled over both single crosses showed statistical differences for all traits, except for PERTLG, PESTLG, and EARLG (Table 11). EARLG did not show any significance in this second set of contrasts because of high interaction with environments. (B73xMo17)F_2 was statistically different from (B73xB84)F_2 for all traits. The same comparison between the (B73xMO17)F_2Syn5 VS (B73xB84)F_2Syn5 was significant for all traits, except for PESTLG and EARLG.

Table 11. Comparisons of the orthogonal contrasts for three sources of variation of the F_2 and F_2 Syn 5 in the single crosses B73 x Mo17 and B73 x B84 for 14 traits evaluated in four environments at Ames (1984, 1985)

Source	df	Mean squares			
		Lodging		Dropped ears	Plant height
		Root	Stalk		
		----------%----------			cm
Progenies/Set	390				
F_2 (A) vs F_2 (B)[b]	10	457.07*	847.29**	16.70*	3908.2**
F_2 S5 (A) vs F_2 S5 (B)	10	515.46*	292.89^{ns}	16.28*	5709.8**
F_2 vs F_2 S5	10	165.43^{ns}	169.20^{ns}	2.81*	8112.8**
Progenies/Set x Env	1170				
F_2 (A) vs F_2 (B)	30	174.65**	205.87**	7.33**	298.54**
F_2 S5 (A) vs F_2 S5 (B)	30	216.57**	139.44**	7.49*	282.75**
F_2 vs F_2 S5	30	88.41**	118.29**	2.67^{ns}	92.49^{ns}
Pooled error	1560				
F_2 (A) vs F_2 (B)	40	48.98	76.13	2.49	81.25
F_2 S5 (A) vs F_2 S5 (B)	40	31.42	31.88	4.25	47.56
F_2 vs F_2 S5	40	35.25	41.92	1.59	100.95

[a]Expressed as the ratio of ear height to plant height.

[b]A = B73 x Mo17 and B = B73 x B84.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

Mean squares						
Ear		Diameter		Ear index[a]	Prolificacy	Kernel depth
Height	Length	Ear	Cob			
cm					no.	cm
373.11**	204.90[ns]	0.256**	1.106**	0.0214**	0.513**	0.222**
363.13**	97.03[ns]	0.316**	1.592**	0.05**	0.759**	0.211**
4240.23**	10.20[ns]	0.227**	0.053**	0.015**	0.121**	0.5**
74.54*	100.12**	0.077**	0.016[ns]	0.00071[ns]	0.027[ns]	0.015*
112.63**	55.31**	0.101**	0.024[ns]	0.00065[ns]	0.038[ns]	0.038[ns]
53.35[ns]	9.53**	0.007*	0.011[ns]	0.0008[ns]	0.014[ns]	0.006[ns]
38.65	0.94	0.018	0.016	0.0005	0.016	0.007
33.26	0.87	0.04	0.03	0.00045	0.015	0.005
44.73	0.89	0.004	0.014	0.0006	0.008	0.005

Table 11. (Continued)

Source	df	Mean squares: Row number	Mean squares: Grain yield	df	Mean squares: Days to silking
		no.	kg ha^{-1}		no.
Progenies/Set	390				
F_2 (A) vs F_2 (B)	10	113.75**	5337.9**	10	71.28**
F_2 S5 (A) vs F_2 S5 (B)	10	140.42**	5305.1*	10	141.25**
F_2 vs F_2 S5	10	13.40**	5271.4**	10	35.53**
Progenies/Set x Env	1170				
F_2 (A) vs F_2 (B)	30	1.01^{ns}	1211.13*	10	3.58^{ns}
F_2 S5 (A) vs F_2 S5 (B)	30	1.49*	1801.8**	10	4.80*
F_2 vs F_2 S5	30	0.92^{ns}	897.4**	10	1.76**
Pooled error	1560				
F_2 (A) vs F_2 (B)	40	0.64	624.44	20	2.47
F_2 S5 (A) vs F_2 S5 (B)	40	0.84	629.56	20	1.47
F_2 vs F_2 S5	40	0.63	301.1	20	0.50

The interactions of S_1 progenies with environments for the F_2 and F_2Syn5 in B73xMo17 were statistically significant for PESTLG, PEDREA, EARLG, and YIELD (Table 10). The F_2Syn5 also showed significant interaction for EARDIM, EARIND, and PROLIF. The F_2Syn5 generation tended to interact more with the environments than the F_2. The F_2 and the F_2Syn5 in B73xB84 showed statistical significance for the interaction of S_1 progenies with environments for PERTLG, PESTLG, PROLIF, and YIELD.

The individual analyses of variance for each environment are presented in Tables A3 to A6 in the Appendix. The design used was effective in removing variation among sets for most of the traits. The differences among sets should be attributed only to environmental effects because each set was composed of random lines.

Progenies/Set was statistically different for all traits in all environments except for PEDREA in environment 2 (Table A4). The F_2 and F_2Syn5 in both single crosses, B73xMO17 and B73xB84, showed statistical differences for all traits except for PERTLG, PESTLG, and PEDREA in some environments. The effects of the environment for YIELD were evident in the trials conducted in 1984. The observed C.V.s also were higher in 1984 compared with 1985. The best environment for YIELD was the Research Center in 1985, and the C.V. was the lowest.

Variance component estimates

The estimates of genetic variances from the analysis of variance combined over environments for the 14 traits measured are included in Table 12. These estimates were calculated for the F_2 and F_2Syn5 gener-

ations in each single cross. The significance of the change in genetic variance was judged by the sum of their respective S.E. The estimates for the two populations in B73xMo17 showed significant increases from F_2 to F_2Syn5 for EARIND and PROLIF. Significant decreases were observed in the estimates for PEDREA, EARDIM, COBDIM, ROWNO, and DAYSIL from the F_2 to F_2Syn5. PTAHE and KERDEP did not show any changes with random mating.

B73xB84, however, showed significant increases in the genetic variance estimates from the F_2 to the F_2Syn5 for PESTLG, EARLG, PROLIF, KERDEP, and YIELD, and decreases for PEDREA. No change was observed for PTAHE. Variation among S_1 progenies of the single crosses showed different performance due to the effects of random mating. Both single crosses were similar in the direction of changes in the genetic variance for PESTLG, EARHE, EARIND, PROLIF, PEDREA, COBDIM, and ROWNO, even though the magnitude of the changes was different. The change in the genetic variance was in the opposite direction for YIELD, PERTLG, DAYSIL, and three yield components, EARLG, EARDIM, and KERDEP. These differences may be due to the different genetic constitution of the two single crosses.

Generally, the genetic estimates for most of the traits were of greater magnitude for the populations derived from B73xMo17. The estimates were significantly different from zero for all traits.

The estimates of the genotype by environment (GxE) variance components from the analysis of variance combined over environments were of relatively low importance for most of the traits and are pre-

Table 12. Genetic variance estimates (σ^2_G) and their standard errors (S.E.) for 14 traits of S_1 progenies of the F_2 and the F_2 Syn 5 generations of two single crosses evaluated in four environments, Ames (1984, 1985)

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	5.316 ± 1.773	3.072 ± 1.313
Stalk lodging, %	28.281 ± 6.352	36.836 ± 7.8
Dropped ears, %	0.363 ± 0.165	-0.038 ± 0.118
Plant height, cm	170.028 ± 26.55	168.623 ± 26.23
Ear height, cm	97.817 ± 15.254	114.105 ± 17.677
Ear length, cm	0.794 ± 0.147	0.685 ± 0.130
Ear diameter, cm	0.0346 ± 0.0056	0.0221 ± 0.0039
Cob diameter, cm	0.014 ± 0.0024	0.0068 ± 0.0013
Ear index[a]	0.00065 ± 0.00011	0.00108 ± 0.00017
Prolificacy, no.	0.0081 ± 0.0014	0.0159 ± 0.0026
Kernel depth, cm	0.0032 ± 0.0006	0.0030 ± 0.0006
Row number, no.	1.389 ± 0.217	0.801 ± 0.132
Yield, kg ha^{-1}	643.802 ± 107.14	526.21 ± 97.21
Days to silking, no.	5.651 ± 0.920	3.929 ± 0.677

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
8.302 ± 3.947	12.131 ± 3.95
2.968 ± 1.606	16.048 ± 3.64
0.121 ± 0.046	0.022 ± 0.032
87.127 ± 14.248	86.831 ± 14.31
50.609 ± 8.177	56.727 ± 9.05
0.648 ± 0.113	0.96 ± 0.16
0.011 ± 0.002	0.0153 ± 0.0027
0.0075 ± 0.0014	0.0066 ± 0.0013
0.00047 ± 0.00008	0.00062 ± 0.0001
0.0035 ± 0.0009	0.0058 ± 0.0012
0.0013 ± 0.0004	0.0023 ± 0.0005
1.422 ± 0.223	1.19 ± 0.19
226.49 ± 45.61	342.168 ± 62.49
2.221 ± 0.415	2.746 ± 0.497

sented in Table 13. Estimates were statistically significant for PERTLG, PESTLG, PEDREA, and YIELD. These traits were expected to show greater G x E interaction because they are more affected by environmental effects. PTAHE, EARHE, COBDIM, EARIND, and DAYSIL were consistent over environments in both single crosses. With regard to PTAHE, EARHE, EARDIM, and YIELD, the F_2Syn5 in both single crosses tended to interact more with environments than the F_2 generation. This performance was evident for YIELD in the single cross B73xMo17. The standard errors for the remaining estimates of the G x E interaction were not statistically different from zero. The lack of significance in the G x E interaction indicates the S_1 progenies were consistent in their performance for the environments sampled.

The error variance estimates are presented in Table 14. The estimates of error variance increased from the F_2 to the F_2Syn5 in B73xMo17 for PEDREA, EARDIM, PROLIF, ROWNO, YIELD, and DAYSIL. With regard to B73xB84, the estimates of error increased for PERTLG, PESTLG, PEDREA, EARLG, COBDIM, and PROLIF from the F_2 to the F_2Syn5 generations. The estimates for genetic variance among S_1 progenies were of greater magnitude than the error variance estimates in B73xMo17 for PTAHE, EARHE, EARDIM, COBDIM, EARIND, ROWNO, YIELD, and DAYSIL. Except for EARDIM, EARIND, and YIELD in B73xB84, the variance among S_1 progenies was greater than the error variance.

The estimates of phenotypic variance are presented in Table 15. The estimates of phenotypic variance were greater in the (B73xMo17)F_2 than in the (B73xMo17)F_2Syn5 for PERTLG, PEDREA, PTAHE, EARLG, EARDIM,

Table 13. Genotype by environment interaction variance estimates and their standard error (S.E.) for 14 traits of S_1 progenies of the F_2 and the F_2 Syn F_5 generations of two single crosses evaluated in four environments, Ames (1984, 1985)

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	12.47 ± 2.30	12.786 ± 1.92
Stalk lodging, %	30.264 ± 5.18	38.289 ± 5.52
Dropped ears, %	1.262 ± 0.26	0.654 ± 0.3
Plant height, cm	5.673 ± 4.25	7.785 ± 3.82
Ear height, cm	0.378 ± 2.52	4.278 ± 2.41
Ear length, cm	0.25 ± 0.08	0.261 ± 0.074
Ear diameter, cm	0.0029 ± 0.0014	0.0032 ± 0.0017
Cob diameter, cm	0.0012 ± 0.0009	0.0012 ± 0.0009
Ear index[a]	0.00004 ± 0.00003	0.00006 ± 0.00003
Prolificacy, no.	0.0003 ± 0.0006	0.0011 ± 0.0009
Kernel depth, cm	0.0003 ± 0.0004	0.0006 ± 0.0004
Row number, no.	0.072 ± 0.034	0.039 ± 0.039
Yield, kg ha^{-1}	73.936 ± 33.58	256.206 ± 48.21
Days to silking, no.	0.303 ± 0.186	0.223 ± 0.212

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
36.077 ± 6.15	17.993 ± 5.35
12.38 ± 2.71	9.059 ± 3.31
0.196 ± 0.072	-0.097 ± 0.082
0.366 ± 4.23	8.43 ± 4.19
0.122 ± 2.16	2.61 ± 1.96
0.093 ± 0.048	0.070 ± 0.048
0.001 ± 0.0013	0.0015 ± 0.0012
0.0018 ± 0.0009	0.0013 ± 0.0009
0.00003 ± 0.00003	0.00007 ± 0.00003
0.0031 ± 0.0008	0.003 ± 0.001
0.0071 ± 0.0005	0.0003 ± 0.0004
0.665 ± 0.049	0.073 ± 0.042
136.868 ± 30.37	140.35 ± 30.15
0.266 ± 0.182	0.235 ± 0.195

Table 14. Error variance estimates and their standard errors (S.E.) for S_1 progenies of the F_2 and the F_2 Syn 5 generations of two single crosses evaluated in four environments, Ames (1984, 1985)

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	24.342 ± 1.81	16.727 ± 1.24
Stalk lodging, %	51.645 ± 3.84	45.932 ± 3.41
Dropped ears, %	2.931 ± 0.22	4.474 ± 0.33
Plant height, cm	68.231 ± 5.07	58.002 ± 4.31
Ear height, cm	43.964 ± 3.27	37.383 ± 2.78
Ear length, cm	1.06 ± 0.079	0.981 ± 0.073
Ear diameter, cm	0.0216 ± 0.0016	0.0252 ± 0.0019
Cob diameter, cm	0.0137 ± 0.001	0.0143 ± 0.0011
Ear index[a]	0.00052 ± 0.00004	0.00054 ± 0.00004
Prolificacy, no.	0.0107 ± 0.0008	0.0137 ± 0.001
Kernel depth, cm	0.0072 ± 0.0005	0.0065 ± 0.0005
Row number, no.	0.517 ± 0.038	0.641 ± 0.048
Yield, kg ha^{-1}	502.779 ± 37.37	518.386 ± 38.53
Days to silking, no.	1.636 ± 0.172	2.041 ± 0.214

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
61.069 ± 4.54	71.974 ± 5.35
32.121 ± 2.39	47.357 ± 3.52
1.021 ± 0.076	1.559 ± 0.12
74.109 ± 5.51	63.748 ± 4.738
37.985 ± 2.82	31.421 ± 9.04
0.738 ± 0.055	0.767 ± 0.057
0.021 ± 0.0016	0.0201 ± 0.0015
0.013 ± 0.001	0.0142 ± 0.0011
0.00056 ± 0.00004	0.00049 ± 0.00004
0.0107 ± 0.0008	0.0132 ± 0.001
0.0071 ± 0.0005	0.0067 ± 0.0005
0.665 ± 0.049	0.657 ± 0.049
361.441 ± 26.87	352.684 ± 62.12
1.644 ± 0.172	1.832 ± 0.192

COBDIM, KERDEP, ROWNO, YIELD, and DAYSIL. The same trend was observed in the (B73xB84)F_2 for PEDREA, COBDIM, and ROWNO. In the B73xB84 single cross, the F_2Syn5 tended to have greater phenotypic variance estimates than the F_2, suggesting a different trend in genetic variability between the two single crosses.

Estimates of heritability

The heritability estimates are presented in Table 16. The lowest values were obtained for PERTLG, PESTLG, and PEDREA for all populations. The low heritability values for these traits could be attributed in part to large error variance estimates (Table 14 and from Tables A2 to A5 in the Appendix) relative to the estimates of genetic variation among S_1 progenies.

In B73xMo17, the traits with the highest heritability estimates included PTAHE, EARHE, ROWNO, EARDIM, and DAYSIL, while in B73xB84, the highest heritability estimates were obtained for ROWNO, EARHE, and PTAHE. All heritability estimates for all traits followed the same trend as that observed for genetic variance estimates since heritability is directly proportional to genetic variance, and G x E interaction was of lesser importance for most of the traits. The estimates of variance components and heritabilities indicated that most of the variability expressed among S_1 progenies for these traits under these environmental conditions was genetic.

The observed changes in the heritability estimates from the F_2 to the F_2Syn5 in B73xMo17 were less than 2% for PTAHE, EARHE, EARLG, and

Table 15. Phenotypic variance estimates and their standard errors (S.R.) (S.E.) for 14 traits of S_1 progenies in the F_2 and the F_2 Syn F_2 generations of two single crosses evaluated in four environments, Ames (1984, 1985)

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	11.476 ± 1.69	8.359 ± 1.23
Stalk lodging, %	42.302 ± 6.24	52.150 ± 7.69
Dropped ears, %	1.045 ± 0.15	0.685 ± 0.10
Plant height, cm	179.975 ± 26.54	177.819 ± 26.22
Ear height, cm	103.407 ± 15.25	119.847 ± 17.67
Ear length, cm	0.989 ± 0.15	0.873 ± 0.13
Ear diameter, cm	0.038 ± 0.006	0.026 ± 0.04
Cob diameter, cm	0.016 ± 0.0024	0.0089 ± 0.0013
Ear index[a]	0.00072 ± 0.00011	0.00116 ± 0.00017
Prolificacy, no.	0.0095 ± 0.0014	0.018 ± 0.003
Kernel depth, cm	0.0042 ± 0.0006	0.0040 ± 0.0006
Row number, no.	1.472 ± 0.02	0.891 ± 0.13
Yield, kg ha^{-1}	725.133 ± 106.92	655.06 ± 96.58
Days to silking, no.	6.211 ± 0.916	4.551 ± 0.671

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
24.955 ± 3.68	25.626 ± 3.78
10.078 ± 1.46	24.232 ± 3.57
0.298 ± 0.04	0.193 ± 0.028
96.483 ± 14.23	96.908 ± 14.29
55.387 ± 8.17	61.306 ± 9.04
0.764 ± 0.11	1.073 ± 0.16
0.0136 ± 0.002	0.018 ± 0.003
0.0096 ± 0.0014	0.0087 ± 0.0013
0.00054 ± 0.00008	0.0007 ± 0.0001
0.0056 ± 0.0008	0.0082 ± 0.0012
0.0023 ± 0.0003	0.0032 ± 0.0005
1.510 ± 0.22	1.291 ± 0.19
305.885 ± 45.1	421.341 ± 62.12
2.765 ± 0.408	3.322 ± 0.490

Table 16. Estimates of heritability (%) on S_1 progeny mean basis for 14 traits in the F_2 and in the F_2 Syn-5 of two single crosses evaluated at Ames (1984, 1985)

	Single crosses					
	B73 x Mo17					
	F_2			F_2 Syn 5		
Traits	h^{2a}	UCI[b]	LCI[c]	h^2	UCI	LCI
Root lodging, %	46.32	60.79	23.86	36.75	53.80	10.28
Stalk lodging, %	66.85	75.79	52.98	70.64	78.55	58.35
Dropped ears, %	34.73	52.32	7.42	---	---	---
Plant height, cm	94.47	95.96	92.16	94.83	96.22	92.66
Ear height, cm	94.59	96.05	92.33	95.21	96.50	93.20
Ear length, cm	80.30	85.61	72.06	78.48	84.28	69.48
Ear diameter, cm	91.00	93.42	87.23	84.85	88.94	78.51
Cob diameter, cm	87.47	90.85	82.23	76.65	82.95	66.88
Ear index[d]	89.58	92.39	85.23	92.87	94.79	89.89
Prolificacy, no.	85.32	89.28	79.18	88.96	91.94	84.34
Kernel depth, cm	77.08	83.26	67.49	76.18	82.60	66.21
Row number, no.	94.39	95.91	92.05	89.90	92.62	85.68
Yield, kg ha^{-1}	88.78	91.81	84.09	80.33	85.63	72.10
Days to silking, no.	90.97	94.05	86.32	86.34	90.99	79.30

[a] h^2 = heritability of S_1 lines on a progeny mean basis.

[b] UCI = upper confidence interval at 0.05 probability level.

[c] LCI = lower confidence interval at 0.05 probability level.

[d] Expressed as the ratio of ear height to plant height.

Single crosses					
B73 x B84					
F_2			F_2 Syn 5		
h^2	UCI	LCI	h^2	UCI	LCI
33.27	51.25	5.34	47.34	61.53	25.30
29.45	48.46	-0.08	66.23	75.33	52.09
40.65	56.65	15.81	11.53	35.38	-25.48
90.30	92.92	86.25	89.60	92.40	85.25
91.37	93.70	87.76	92.53	94.54	89.41
84.89	88.96	78.57	89.45	92.29	85.03
78.88	84.57	70.04	84.20	88.46	77.59
78.46	84.27	69.45	75.93	82.42	65.86
85.91	89.71	80.02	88.73	91.77	84.01
62.36	72.51	46.61	70.88	78.73	58.70
58.15	69.43	40.64	71.60	79.25	59.71
94.20	95.76	91.77	92.22	94.31	88.96
74.04	81.04	63.18	81.21	86.27	73.35
80.33	87.02	70.18	82.68	88.57	73.74

KERDEP, and were greater than 5% for EARDIM, COBDIM, and YIELD. The observed changes in the heritability estimates from the F_2 to the F_2Syn5 in B73xB84 were less than 2% for PTAHE, EARHE, and ROWNO, while the traits with changes greater than 5% included EARDIM, EARIND, PROLIF, KERDEP, and YIELD. The comparisons for changes in heritability for PERTLG, PESTLG, and PEDREA, were excluded because of low precision in the estimates.

The genetic and phenotypic variance estimates for each environment are presented in Tables A12 to A19 in the Appendix. The most obvious trends among environments were the changes observed for YIELD, from F_2 to F_2Syn5, because the estimates decreased in environments 1 and 2 (1984; Tables A12 and A13) and increased in environments 3 and 4 (1985; Tables A14 and A15), suggesting an interaction with environments (Tables 10 and 13). In B73xB84, there was a slight decrease from the F_2 to the F_2Syn5 in environment 2 (Table A13), but an increase for the other environments (Tables A12, A14, and A15). For EARHE, EARIND, and PROLIF, there was always an increase in the genetic variance from the F_2 to the F_2Syn5 in both single crosses. PTAHE showed a slight decrease in B73xMo17 in environments 1, 3, and 4, and a slight increase in environment 2, while in B73xB84 there was a decrease in environment 1, but an increase in the other environments. For EARLG and EARDIM, there was always a decrease in B73xMo17 but an increase in B73xB84. Similar patterns occurred for the phenotypic variance estimates.

The genetic coefficients of variability (GCV) are shown in Table 17. There was an increase in the GCVs from the F_2 to the F_2Syn5 for

PERTLG, PESTLG, PTAHE, EARHE, EARIND, and PROLIF, but a decrease for ROWNO in both single crosses. For the other traits, there was a decrease in B73xMo17 but an increase in B73xB84. Most of the changes were less than 1%, except for PERTLG, PESTLG, PEDREA, PROLIF, ROWNO, and YIELD. The greatest change in YIELD was observed from the F_2 to the F_2Syn5 in B73xB84 (8.06%). This change is explained by the increase in genetic variance from the F_2 to the F_2Syn5. The small decrease in GCV in B73xMo17 is explained by the decrease in both mean and genetic variance because these estimates reflect the changes that occurred for both means and the genetic standard error associated with that trait.

Genotypic and phenotypic correlations

The estimates of genetic correlations for the F_2 and the F_2Syn5 generations of each single cross are shown in Tables 18 and 19. Correlation computations were based on plot means of the 100 S_1 lines evaluated in four environments. For B73xMo17, there was no shift in the genotipic correlations among the pairs of traits for PERTLG - (PEDREA, PTAHE, EARHE, and EARIND); PESTLG - (EARHE, EARLG, ROWNO, COBDIM, and PROLIF); PEDREA - (EARLG, ROWNO, COBDIM, and KERDEP); PTAHE - (EARHE, EARDIM, and DAYSIL); EARHE - (EARLG, COBDIM, and EARIND); EARLG - (ROWNO, EARIND, KERDEP); ROWNO - (YIELD, and DAYSIL); EARDIM - (PROLIF and KERDEP); COBDIM - DAYSIL. Similar correlations for the F_2 and F_2Syn5 generations suggest that random mating did not change the genetic relation of the traits measured. It seems linkage and (or)

Table 17. Genetic coefficients of variability (%) estimated for 14 traits based on trials conducted in four environments

Traits	Single crosses			
	B73 x Mo17		B73 x B84	
	F_2	F_2 Syn 5	F_2	F_2 Syn 5
Root lodging, %	94.18	99.34	58.28	72.04
Stalk lodging, %	66.01	86.65	34.91	71.04
Dropped ears, %	85.30	---	143.93	76.77
Plant height, cm	6.71	6.99	5.04	5.34
Ear height, cm	10.28	12.00	7.44	8.43
Ear length, cm	5.54	5.31	5.81	6.96
Ear diameter, cm	4.28	3.41	2.37	2.80
Cob diameter, cm	4.49	3.17	3.10	2.90
Ear index[a]	5.13	6.84	4.17	4.85
Prolificacy, no.	9.64	13.92	5.66	7.42
Kernel depth, cm	6.63	6.28	4.64	5.93
Row number, no.	7.88	5.88	7.20	6.41
Yield, kg ha^{-1}	51.37	49.46	32.55	40.61
Days to silking, no.	2.80	2.37	1.72	1.92

[a]Expressed as the ratio of ear height to plant height.

Table 18. Genetic correlations among 14 traits between the F_2 and F_2 Syn 5 derived from the single cross B73 x Mo17 based on 100 S_1 lines evaluated in four environments at Ames (1984, 1985)[1]

Traits	Stalk lodging		Dropped ears		Plant height		Ear height	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	-0.06	0.27*	0.07	0.05	0.41	0.40	0.45	0.41
Stalk lodging			-0.13	-0.20	0.05	0.13	0.14	0.13
Dropped ears					-0.13	0.02	-0.11	0.12
Plant height							0.81	0.80
Ear height								
Ear length								
Row number								
Ear diameter								
Cob diameter								
Prolificacy								
Ear index								
Kernel depth								
Grain yield								

*Indicates that the shift from F_2 to F_2 Syn 5 was significant at the 0.05 probability level.

Ear length		Row number		Ear diameter		Cob diameter		Prolificacy	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
0.09	0.01	0.27	0.19	0.13	0.03	0.20	-0.09*	-0.05	0.56*
0.19	0.18	-0.05	-0.06	0.10	0.01	0.02	-0.01	0.34	0.37
0.00	-0.05	0.01	0.03	0.02	0.11	0.01	0.06	-0.18	-0.13
0.16	0.26	-0.08	-0.20	0.00	0.06	0.10	-0.04	-0.05	0.22*
0.26	0.31	-0.04	-0.17	-0.02	0.18	0.10	0.05	0.06	0.34*
		-0.29	-0.28	-0.25	-0.05	-0.34	-0.08	0.24	0.02
				0.66	0.40*	0.60	0.32*	-0.15	0.02
						0.62	0.41*	-0.09	-0.07
								-0.24	-0.05

Table 18. (Continued)

Traits	Ear index		Kernel depth		Grain yield		Days to silking	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	0.32	0.31	0.00	0.09	-0.15	0.40*	0.43	0.09*
Stalk lodging	0.22	0.09	0.11	0.01	0.20	0.42	-0.05	-0.17
Dropped ears	-0.04	0.20	0.02	0.08	-0.16	-0.01	0.10	0.24
Plant height	0.43	0.52	-0.09	0.10	-0.11	0.23*	0.57	0.52
Ear height	0.73	0.79	-0.12	0.18*	-0.02	0.36*	0.59	0.46
Ear length	0.29	0.29	-0.04	0.00	0.29	0.09	0.03	0.17
Row number	0.02	-0.11	0.37	0.26	0.11	0.11	0.01	0.02
Ear diameter	-0.03	0.27*	0.60	0.63	0.27	0.21	-0.11	0.14
Cob diameter	0.07	0.14	0.17	0.09	-0.10	0.07	0.15	0.16
Prolificacy	0.18	0.36	0.09	-0.05	0.59	0.68	-0.34	-0.20
Ear index			-0.10	0.22*	0.11	0.39*	0.40	0.29
Kernel depth					0.46	0.20*	-0.28	0.05*
Grain yield							-0.49	-0.22*

epistasis were not important factors influencing the relation of traits in these populations.

The greatest and significant shifts occurred among the following pairs of traits: PERTLG - (PESTLG, COBDIM, PROLIF, YIELD, and DAYSIL); PTAHE - (PROLIF and YIELD); EARHE - (PROLIF, KERDEP, and YIELD); ROWNO - (EARDIM and COBDIM); EARDIM - (EARIND and COBDIM); EARIND - (KERDEP and YIELD); KERDEP - (YIELD and DAYSIL); YIELD - DAYSIL. The significant shifts suggest there was recombination between YIELD and several traits. These shifts were of greater magnitude (> 0.30); for PTAHE, the correlation changed from -0.11 in F_2 to 0.23 in F_2Syn5; for EARHE, the coefficient changed from -0.02 to 0.36; and for EARIND, the shift was from 0.11 to 0.39. There was a decrease in the correlation coefficient for the following pairs of traits: KERDEP changed from 0.46 in F_2 to 0.20 in F_2Syn5. This same trend was observed for the following pairs of traits: DAYSIL - (PERTLG, PROLIF, and EARIND).

Some shifts were observed to increase from the F_2 to the F_2Syn5, while some decreased. No association was found between PERTLG and PEDREA, PERTLG and EARLG, PEDREA and KERDEP, PEDREA and EARLG, EARLG and KERDEP, PROLIF and EARDIM, and PROLIF and KERDEP.

For B73xB84, there were no observed shifts in the genetic correlation coefficients from the F_2 to the F_2Syn5 among the following pairs of traits: YIELD - (PERTLG, PTAHE, EARHE, EARLG, ROWNO, COBDIM, and EARIND). The 10 largest and significant shifts in the genetic correlation coefficients from the F_2 to the F_2Syn5 were observed among the following pairs of traits: PERTLG - (PEDREA and PTAHE); PESTLG -

Table 19. Genetic correlations among 14 traits between the F_2 and F_2 Syn 5 derived from the single cross B73 x B84 based on 100 S_1 lines evaluated in four environments at Ames (1984, 1985)[1]

Traits	Stalk lodging		Dropped ears		Plant height		Ear height	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	0.01	0.18	-0.18	0.11*	0.11	0.41*	0.20	0.42
Stalk lodging			-0.06	0.05	0.09	0.30	0.20	0.31
Dropped ears					-0.08	-0.07	-0.15	-0.02
Plant height							0.74	0.75
Ear height								
Ear length								
Row number								
Ear diameter								
Cob diameter								
Prolificacy								
Ear index								
Kernel depth								
Grain yield								

*Indicates that the shift from F_2 to F_2 Syn 5 was significant at the 0.05 probability level.

Ear length		Row number		Ear diameter		Cob diameter		Prolificacy	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
0.05	0.18	-0.20	-0.28	-0.01	-0.06	0.01	0.02	0.20	0.07
-0.03	-0.02	-0.13	-0.27	0.13	-0.28*	0.07	-0.08	0.01	0.28
-0.03	-0.03	-0.10	-0.19	-0.16	0.00	-0.25	0.01	0.09	0.08
0.06	0.20	0.17	-0.33*	0.22	0.06	0.19	-0.02	0.17	0.19
-0.04	0.12	0.08	-0.33*	0.12	-0.04	0.17	-0.02	0.34	0.30
		-0.11	-0.23	0.16	-0.01	-0.19	-0.18	-0.29	0.11*
				0.37	0.45	0.33	0.33	-0.22	-0.23
						0.47	0.29	-0.29	-0.19
								-0.17	-0.26

Table 19. (Continued)

Traits	Ear index		Kernel depth		Grain yield		Days to silking	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	0.21	0.23	-0.02	-0.07	0.10	0.03	0.05	0.23
Stalk lodging	0.23	0.19	0.09	-0.24*	0.12	0.04	-0.14	0.05
Dropped ears	-0.18	0.06	0.03	-0.01	0.17	-0.09	-0.13	-0.16
Plant height	0.30	0.28	0.09	0.08	0.09	0.09	0.28	0.46
Ear height	0.63	0.66	-0.02	-0.03	0.12	0.10	0.17	0.51*
Ear length	-0.15	-0.03	0.35	0.11	0.38	0.37	0.04	-0.03
Row number	-0.04	-0.18	0.14	0.26	-0.08	-0.06	0.15	-0.09
Ear diameter	-0.06	-0.14	0.44	0.66*	0.15	0.23	-0.04	-0.14
Cob diameter	0.07	0.00	0.09	0.05	-0.15	-0.19	0.10	0.17
Prolificacy	0.38	0.28	-0.18	-0.04	0.28	0.45	-0.13	0.06
Ear index			-0.13	-0.15	0.09	0.04	-0.04	0.36*
Kernel depth					0.30	0.36	-0.14	-0.25
Grain yield							-0.40	-0.22

(EARDIM and KERDEP); PTAHE - ROWNO; EARHE - (ROWNO and DAYSIL); EARLG - PROLIF; EARIND - DAYSIL; and EARDIM - KERDEP. There were 41 smaller shifts in the genetic correlation coefficients from the F_2 to the F_2Syn5; these changes ranged from 0.08 to 0.20 in absolute value. The largest shifts were greater than 0.25 in absolute value.

The estimates of phenotypic correlations among traits for the F_2 to F_2Syn5 generations are presented in Tables 20 and 21. The greatest (and significant) phenotypic correlation coefficients in B73xMo17 were observed between the following pairs of traits: PERTLG - (PTAHE and EARHE); PESTLG - PROLIF; PTAHE - (EARHE, EARIND, and DAYSIL); EARHE - (EARLG, EARIND, and DAYSIL); ROWNO - (EARDIM, COBDIM, and KERDEP); EARDIM - (COBDIM, KERDEP, and YIELD); PROLIF - YIELD; EARIND - DAYSIL; and KERDEP - YIELD. There were shifts either from significant to non-significant or vice versa from F_2 to F_2Syn5 for PERTLG - (ROWNO, COBDIM, PROLIF, YIELD, and DAYSIL); PESTLG - (PEDREA, EARLG, EARIND); PTAHE - (EARLG, PROLIF, and YIELD); EARHE - (EARDIM, PROLIF, KERDEP, and YIELD); EARLG - (COBDIM, PROLIF, and YIELD); EARDIM - EARIND; COBDIM - PROLIF; PROLIF - DAYSIL; and EARIND - (KERDEP and YIELD). No significant changes were found between PEDREA and all the other traits; PEDREA was not associated with all these traits. There were significant shifts (14) for PERTLG - (PESTLG, COBDIM, PROLIF, YIELD, and DAYSIL); PTAHE - (PROLIF and YIELD); EARHE - (KERDEP and YIELD); ROWNO - (EARDIM and COBDIM); EARIND - YIELD; KERDEP - DAYSIL; YIELD - DAYSIL.

The highest phenotypic correlation coefficients for the B73xB84

Table 20. Phenotypic correlations among 14 traits between the F_2 and F_2 Syn 5 derived from the single cross B73 x Mo17 based on 100 S_1 lines evaluated in four environments at Ames (1984, 1985)[1]

Traits	Stalk lodging		Dropped ears		Plant height	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	-0.14	0.18[a]	0.05	0.16	0.45**	0.38**
Stalk lodging			-0.13	-0.23*	0.07	0.13
Dropped ears					-0.08	0.08
Plant height						
Ear height						
Ear length						
Row number						
Ear diameter						
Cob diameter						
Prolificacy						
Ear index						
Kernel depth						
Grain yield						

[a]Indicates that the shift from F_2 to F_2 S5 (F_2 Syn 5) was significant at the 0.05 probability level.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

Ear height		Ear length		Row number		Ear diameter	
F_2	F_2 S5	F_2		F_2	F_2 S5	F_2	F_2 S5
0.48**	0.40**	0.03	0.06	0.28**	0.16	0.13	0.01
0.15	0.16	0.21*	0.15	-0.04	-0.05	0.08	0.02
-0.04	0.14	0.03	-0.03	0.04	0.08	0.00	0.15
0.88**	0.87**	0.14	0.30**	-0.08	-0.18	0.01	0.12
		0.24*	0.30**	-0.03	-0.14	-0.02	0.02
				-0.26*	-0.28**	-0.11	0.04
						0.73**	0.50**[a]

Table 20. (Continued)

Traits	Cob diameter		Prolificacy		Ear index	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	-0.24*	-0.08[a]	-0.04	0.50**[a]	0.34	0.29**
Stalk lodging	-0.01	-0.01	0.34**	0.41**	0.22*	0.13
Dropped ears	-0.07	0.03	-0.15	-0.07	0.02	0.17
Plant height	0.10	-0.02	-0.01	0.27**[a]	0.43**	0.53**
Ear height	0.10	0.07	0.11	0.39**[a]	0.80**	0.87**
Ear length	-0.28**	-0.07	0.21*	0.28**	0.24*	0.10
Row number	0.64**	0.39**[a]	-0.15	0.06	0.04	-0.07
Ear diameter	0.68**	0.53**	-0.09	-0.01	-0.03	0.29**
Cob diameter			-0.24*	-0.02	0.06	0.17
Prolificacy					0.22*	0.41**
Ear index						
Kernel depth						
Grain yield						

Kernel depth		Grain yield		Days to silking	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
-0.03	0.06	-0.14	0.37**[a]	0.44**	0.09[a]
0.12	0.02	0.25*	0.45**	-0.09	-0.15
0.06	0.15	-0.06	0.04	0.10	0.18
-0.08	0.15	-0.05	0.30**[a]	0.57**	0.54**
-0.11	0.21*[a]	0.03	0.41**[a]	0.58**	0.48**
0.10	0.10	0.38**	0.20	0.01	0.17
0.43**	0.32**	0.11	0.16	0.00	0.02
0.77**	0.82**	0.30**	0.29**	-0.11	0.14
0.05	-0.04	-0.10	0.08	0.16	0.19
0.09	0.01	0.69**	0.82**	-0.37**	-0.20
-0.01	0.23*	0.13	0.43**[a]	0.39**	0.30**
		0.50**	0.29**	-0.29**	0.04[a]
				-0.53**	-0.25*[a]

generations were among the following pairs of traits: PERTLG - ROWNO; PTAHE - (EARHE, EARIND, and DAYSIL); EARHE - (PROLIF and EARIND); EARLG - **YIELD**; ROWNO - (EARDIM, COBDIM, and PROLIF); EARDIM - (COBDIM and KERDEP); COBDIM - KERDEP; PROLIF - (EARIND and **YIELD**); KERDEP - **YIELD**; and DAYSIL - **YIELD**; these coefficients were statistically significant. The 12 greatest and significant changes from F_2 to F_2Syn5 were observed between the following pairs of traits (some from significant to nonsignificant, or vice versa): DAYSIL - (EARHE and EARIND); **YIELD** - PEDREA; KERDEP - (EARLG and EARDIM); PROLIF - EARLG; COBDIM - PEDREA; EARDIM - PESTLG; ROWNO - (PTAHE and EARHE); EARHE - PERTLG; and PTAHE - PERTLG. These changes suggest that recombination has occurred. It seems that random mating changed the genetic constitution among the traits in each population; that each population had different amount of linkages among the traits; and that the amount of genetic disequilibrium was different in each population.

S_1 mean analyses between populations

Mean values and coefficients of variation for all traits measured in F_2 and F_2Syn5 in each individual trial for each single cross are presented in Tables A7 to A10 in the Appendix. In Tables A7 to A9, the C.V.s tended to be higher in F_2Syn5 rather than in F_2 for the single cross B73xMo17.

The observed change in the means from the F_2 to the F_2Syn5 for all traits in each individual environment are presented in Table A11 in the Appendix. The means of the S_1 progenies for each population were

Table 21. Phenotypic correlations among 14 traits between the F_2 and F_2 Syn 5 derived from the single cross B73 x B84 based on 100 S_1 lines evaluated in four environments at Ames (1984, 1985)[1]

Traits	Stalk lodging		Dropped ears		Plant height	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	-0.11	0.15	-0.23*	0.00	0.15	0.44**[a]
Stalk lodging			-0.18	0.01	0.10	0.31**
Dropped ears					-0.04	-0.13
Plant height						
Ear height						
Ear length						
Row number						
Ear diameter						
Cob diameter						
Prolificacy						
Ear index						
Kernel depth						
Grain yield						

[a]Indicates that the shift from F_2 to F_2 S5 (F_2 Syn 5) was significant at the 0.05 probability level.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

Ear height		Ear length		Row number		Ear diameter	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
0.20	0.46**[a]	0.02	0.15	-0.23*	-0.27**	-0.06	-0.11
0.17	0.33**	-0.10	-0.01	-0.07	-0.26*	0.11	-0.23*[a]
-0.09	-0.06	-0.03	-0.02	-0.04	-0.15	-0.11	-0.04
0.83**	0.83**	0.09	0.22*	0.15	-0.30**[a]	0.24*	0.09
		-0.08	0.11	0.04	-0.34**[a]	0.07	-0.04
				-0.10	-0.21*	0.26*	0.09
						0.46**	0.50**

Table 21. (Continued)

Traits	Cob diameter		Prolificacy		Ear index	
	F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
Root lodging	-0.05	0.01	0.19	0.04	0.15	0.26*
Stalk lodging	0.10	-0.09	0.04	0.30**	0.16	0.21*
Dropped ears	-0.35**	-0.08[a]	0.18	0.02	-0.12	0.04
Plant height	0.15	0.01	0.16	0.23*	0.27**	0.26*
Ear height	0.10	-0.01	0.34**	0.33**	0.76**	0.75**
Ear length	-0.11	-0.06	-0.24*	0.14[a]	-0.24*	-0.07
Row number	0.37**	0.34**	-0.22*	-0.23*	-0.08	-0.23*
Ear diameter	0.54**	0.38**	-0.27*	-0.17	-0.15	-0.19
Cob diameter			-0.19	-0.18	-0.01	-0.03
Prolificacy					0.42**	0.30**
Ear index						
Kernel depth						
Grain yield						

Kernel depth		Grain yield		Days to silking	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5
-0.03	-0.12	0.06	0.00	0.05	0.28**
0.03	-0.19	0.12	0.04	-0.12	0.06
0.18	0.00	0.15	-0.13[a]	-0.09	-0.16
0.14	0.09	0.12	0.13	0.25*	0.47**
0.00	-0.04	0.13	0.10	0.16	0.54**
0.40**	0.13[a]	0.44**	0.44**	-0.02	-0.05
0.19	0.31**	-0.08	-0.03	0.16	-0.10
0.67**	0.81**[a]	0.17	0.27**	-0.08	-0.15
-0.27*	-0.23*	-0.19	-0.11	0.08	0.10
-0.13	-0.07	0.46**	0.57**	-0.20	0.02
-0.16	-0.18	0.09	0.01	-0.01	0.38**[a]
		0.36**	0.36**	-0.16	-0.22*
				-0.52**	-0.31**

expressed as the percentage of the F_2 in each single cross.

PERTLG increased in 1984 in (B73xMo17)F_2Syn5 but decreased in 1985, indicating this trait was influenced by the environment. PESTLG, PTAHE, EARHE, EARLG, COBDIM, EARIND, PROLIF, and YIELD were lower in (B73xMo17)F_2Syn5.

PERTLG, PTAHE, EARHE, EARIND, PROLIF, and YIELD decreased in mean from the F_2 to the F_2Syn5 in B73xB84; EARLG, EARDIM, COBDIM, KERDEP, and ROWNO increased slightly in F_2Syn5.

Some traits had the same trend from the F_2 to F_2Syn5 generations in both single crosses. The effects of random mating, therefore, were similar for PTAHE, EARHE, EARIND, PROLIF, KERDEP, ROWNO, and YIELD.

The means, ranges, and tests of normality of the F_2 and the F_2Syn5 of the S_1 progenies of B73xMo17 and of B73xB84 are listed in Tables 22 and 23. S_1 progeny distributions for the F_2 and F_2Syn5 for YIELD, EARHE, EARLG, EARDIM, and DAYSIL for both single crosses are depicted in Figures 10 to 19.

The means of 100 S_1 progenies derived from the F_2 in B73xMo17 were significantly greater than F_2Syn5 for PERTLG, PESTLG, PTAHE, EARHE, EARLG, COBDIM, PROLIF, EARIND, YIELD, and DAYSIL. The greatest differences between the means were observed for PERTLG, PESTLG, EARHE, and YIELD. EARHE decreased 7.29% and PTAHE decreased 4.12%. YIELD decreased 6.18% from the F_2 to the F_2Syn5 (Fig.10). The range for YIELD was reduced and some increase in the frequency for values below the mean were observed. EARHE had a change in the F_2Syn5 toward lower values (Fig. 12), which can be considered as favorable. The decrease

Table 22. Mean comparisons and normality tests between the F_2 and F_2 Syn 5 for 14 traits in the single cross B73 x Mo17 evaluated in four environments at Ames (1984, 1985)

Traits	Mean		Diff[a]	Min		Max	
	F_2	F_2 S5		F_2	F_2 S5	F_2	F_2 S5
Root lodging, %	2.45	1.76	-28.16*[c]	0.00	0.00	16.2	16.7
Stalk lodging, %	8.05	7.00	-13.04*	0.6	0.00	44.8	35.9
Dropped ears, %	0.71	0.80	12.68[ns]	0.00	0.00	5.1	3.58
Plant height, cm	194	186	-4.12*	164	145	226	214
Ear height, cm	96	89	-7.29*	71	55	117	117
Ear length, cm	16.1	15.6	-3.11*	12.9	13.3	18.4	18.3
Row number, no.	15	15.2	1.33*	12	12.9	18.5	17.6
Ear diameter, cm	4.35	4.37	0.46[ns]	3.86	3.93	4.89	4.71
Cob diameter, cm	2.63	2.61	-0.76*	2.31	2.37	2.98	2.79
Prolificacy, no.	0.94	0.91	-3.19*	0.50	0.46	1.21	1.48
Ear index[f]	0.50	0.48	-4.0*	0.43	0.38	0.55	0.55
Kernel depth, cm	0.86	0.88	2.33*	0.70	0.66	1.05	1.02
Grain yield, kg ha^{-1}	4939	4634	-6.18*	2030	2056	7117	6303
Days to silking, no.	84.8	83.7	-1.30*	79.3	79.5	92.8	89.0

[a]Expressed as the superiority of F_2 as compared to F_2 Syn 5 (in percent)

[b]1, 2 indicates F_2 and F_2 Syn 5, respectively.

[c]*, ns indicates significance at 0.05 probability level and nonsignificance, respectively.

[d]* indicates that the test of normality is rejected.

[e]NS indicates that the population is distributed as normal.

[f]Expressed as the ratio of ear height to plant height.

Range		Skewness		Kurtosis		Normality	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	1[b]	2[b]
16.2	16.7	2.32	2.80	5.83	8.80	*[d]	*
44.2	35.9	2.07	1.88	7.45	3.69	*	*
5.1	3.58	2.33	1.17	6.32	1.13	*	*
62	69	0.05	-0.15	-0.23	0.26	NS[e]	NS
47	62	-0.15	-0.25	-0.26	0.35	NS	NS
5.5	5.0	-0.28	0.26	0.76	0.24	NS	NS
6.5	4.7	0.45	0.24	0.53	0.15	*	*
1.04	0.79	0.31	-0.34	-0.21	-0.07	NS	NS
0.66	0.42	0.12	-0.35	0.11	-0.52	NS	NS
0.71	1.02	-0.84	0.44	3.62	5.14	NS	*
0.12	0.17	-0.22	-0.33	-0.37	0.07	NS	NS
0.35	0.36	0.25	-0.39	-0.08	0.71	NS	NS
5088	4248	-0.47	-0.70	1.27	0.91	NS	*
13.5	9.5	0.68	0.34	0.87	-0.61	*	*

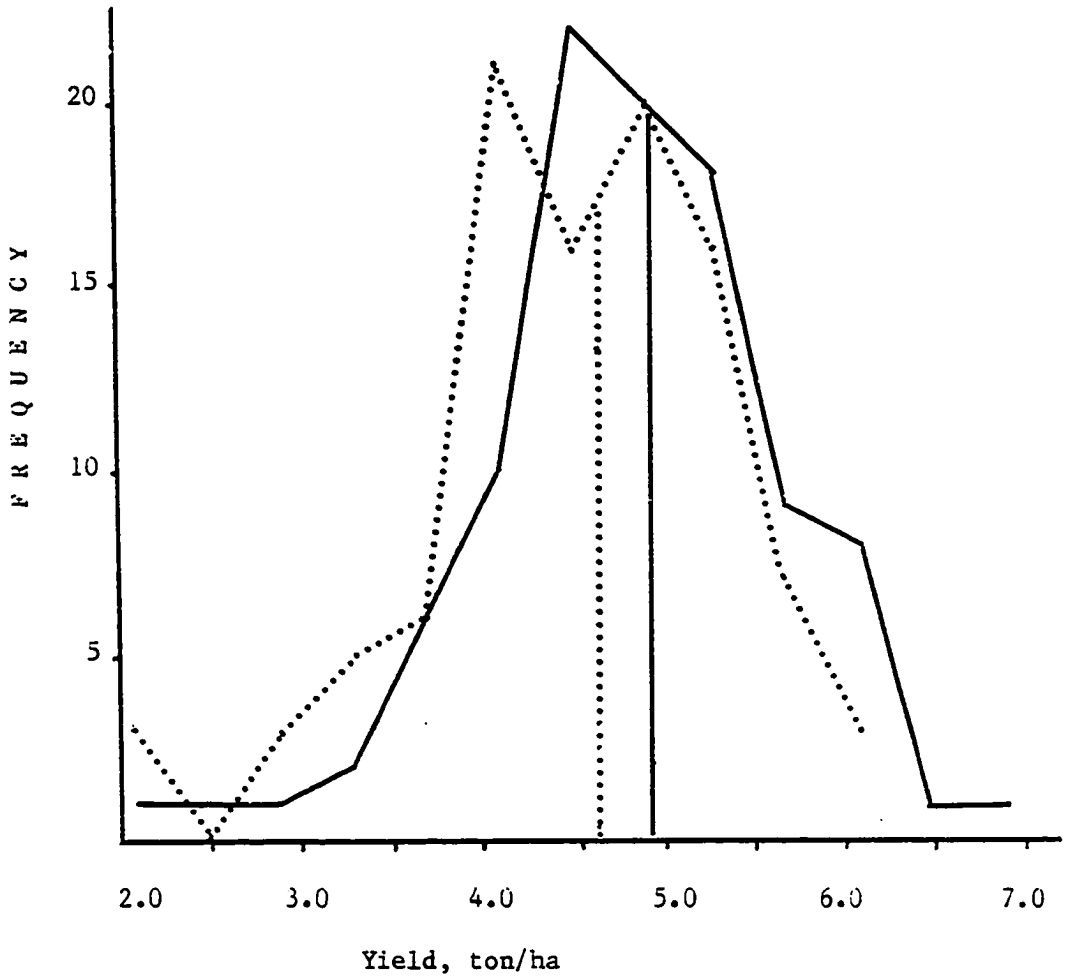

Figure 10. Frequency distributions and means for yield for 100 S_1 progenies for the F_2(___) and F_2Syn5(...) populations from the B73xMo17 cross evaluated in four environments

in EARHE was similar to that observed for YIELD. EARLG had a decrease of 3.11% (Fig. 14), a decrease in range, and a shift toward lower values; the F_2 had a higher frequency of low values. EARDIM did not change significantly, but the F_2Syn5 tended to have higher frequency of values above the mean; the range also decreased in frequency of low and high values (Fig. 16). DAYSIL had a reduced range in F_2Syn5, as well as a reduction in the mean of 1.3% (Fig. 18). With respect to minimum values, the F_2Syn5 showed lower values than the F_2 for all traits, except for EARLG, EARDIM, COBDIM, ROWNO, YIELD, and DAYSIL. The maximum values in F_2 were superior to those in F_2Syn5 for most of the traits, except for PERTLG and PROLIF. This superiority represents an advantage only for EARDIM and YIELD, where higher values are desirable. Greater ranges were observed in the F_2Syn5 for PERTLG, PTAHE, EARHE, PROLIF, and EARIND, but this range included lower values, so there was not an advantage in the range if we deal with selection for these traits. The advantage would be for PESTLG, PEDREA, PTAHE, EARHE, and COBDIM because lower values are desirable.

PERTLG was more positively skewed and more highly peaked in the F_2Syn5 than in F_2. For PROLIF, the F_2Syn5 was also more peaked than the F_2 and slightly skewed to the right. The test of normality was rejected in both populations for PERTLG, PESTLG, PEDREA, ROWNO, and DAYSIL, and for only PROLIF and YIELD in the F_2Syn5. Most of the traits had a trend to regress to lower values.

The B73xB84 means in F_2 were greater for PERTLG, PEDREA, PTAHE, EARHE, PROLIF, EARIND, and YIELD, than those in F_2Syn5. The greatest

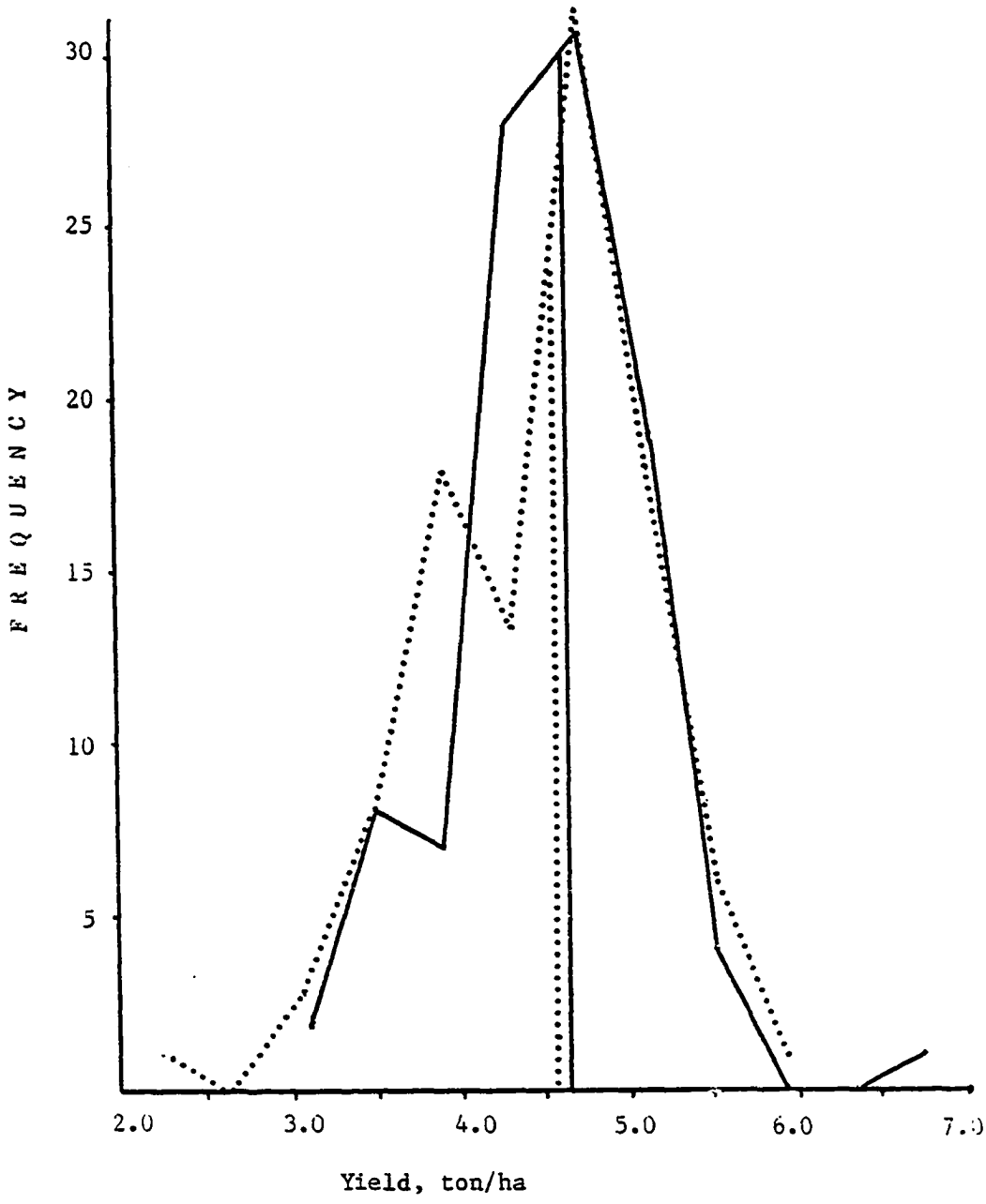

Figure 11. Frequency distributions and means for yield for 100 S_1 progenies for the F_2(___) and F_2Syn5(...) populations from the B73xB84 cross evaluated in four environments

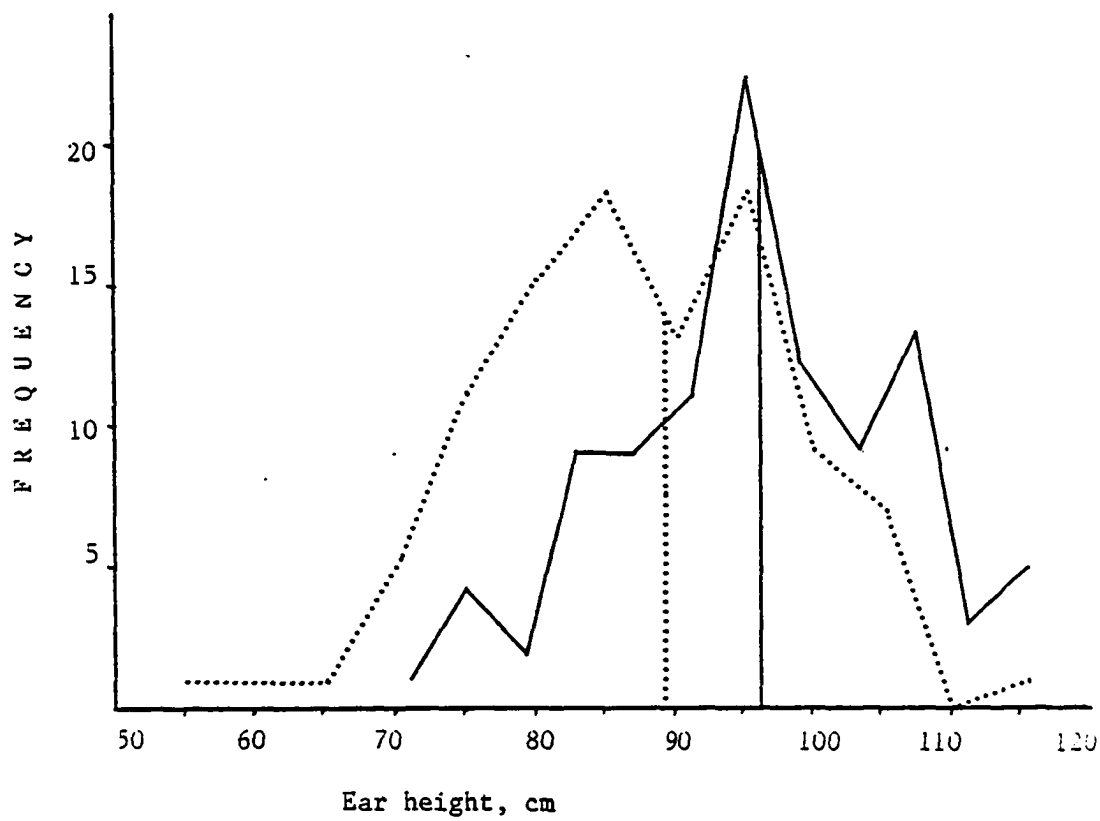

Figure 12. Frequency distributions and means for ear height for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xMo17 cross evaluated in four environments

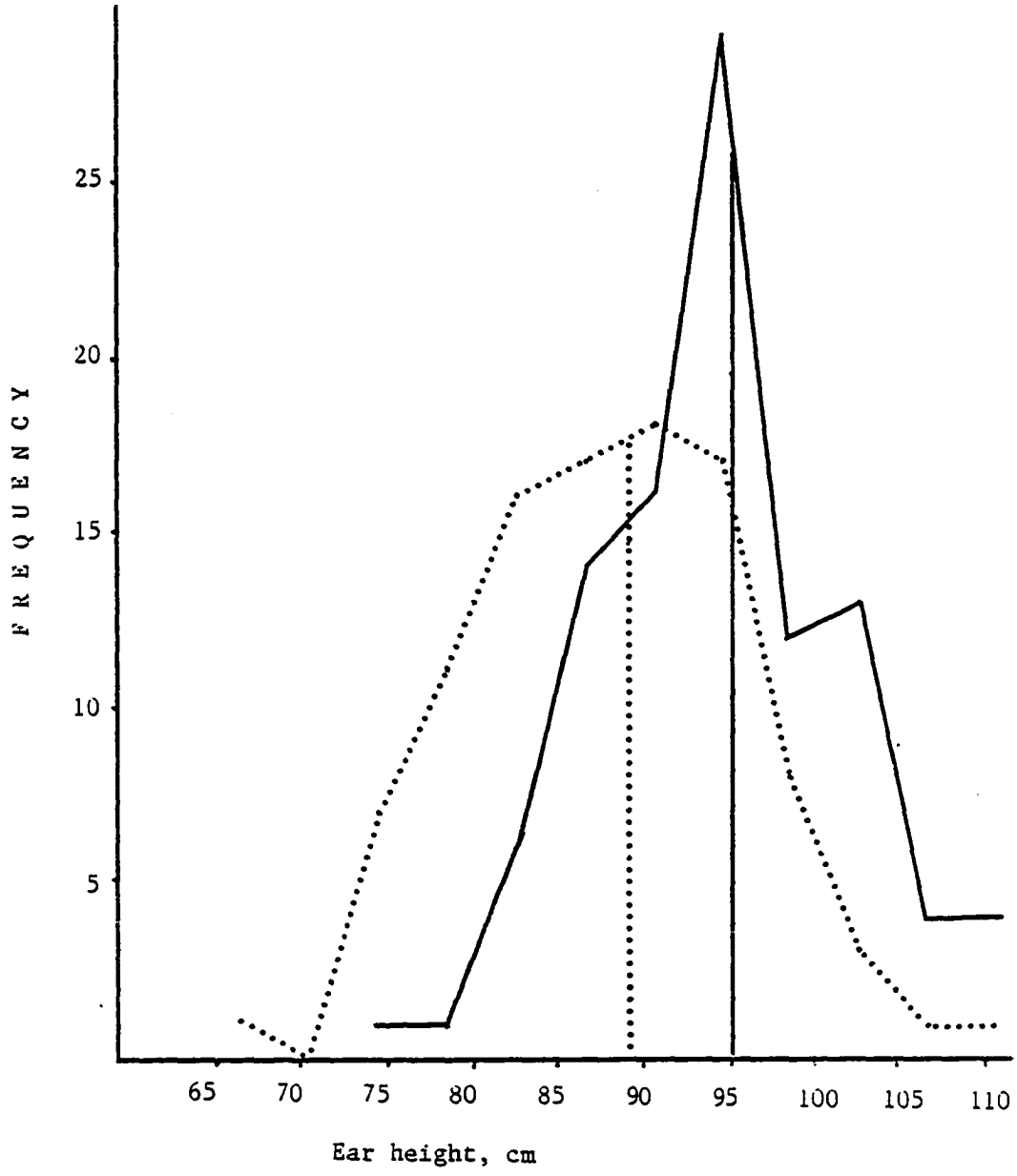

Figure 13. Frequency distributions and means for ear height for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xB84 cross evaluated in four environments

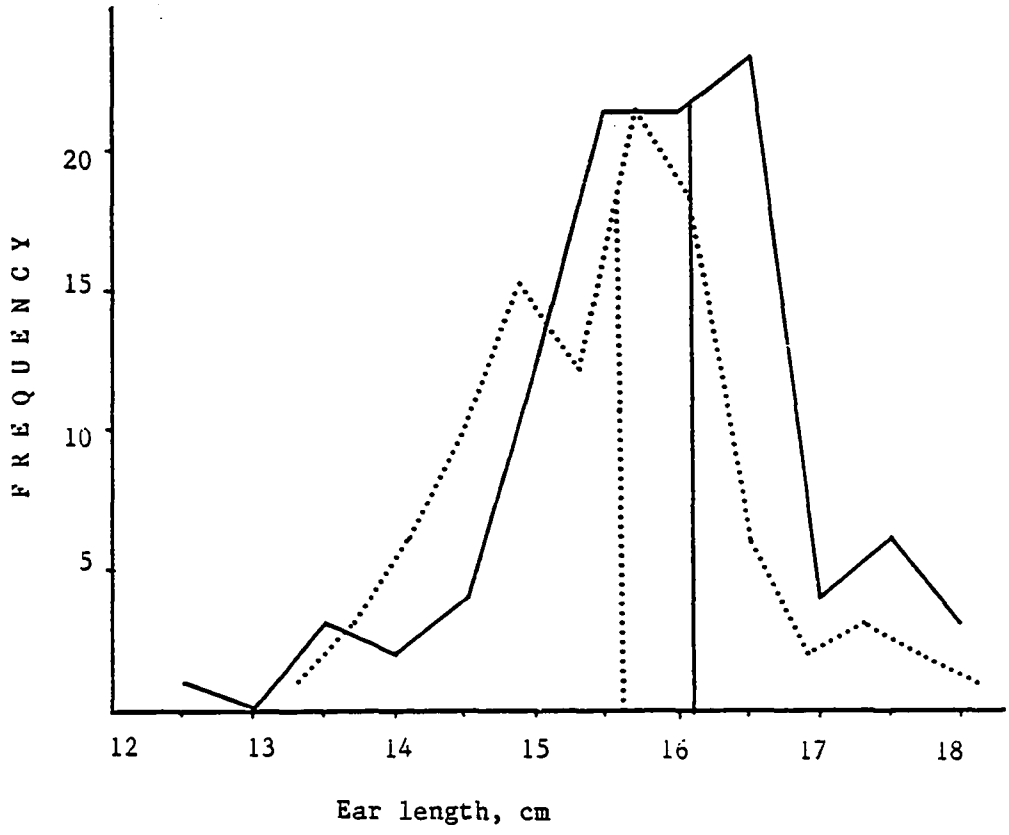

Figure 14. Frequency distributions and means for ear length for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xMo17 cross evaluated in four environments

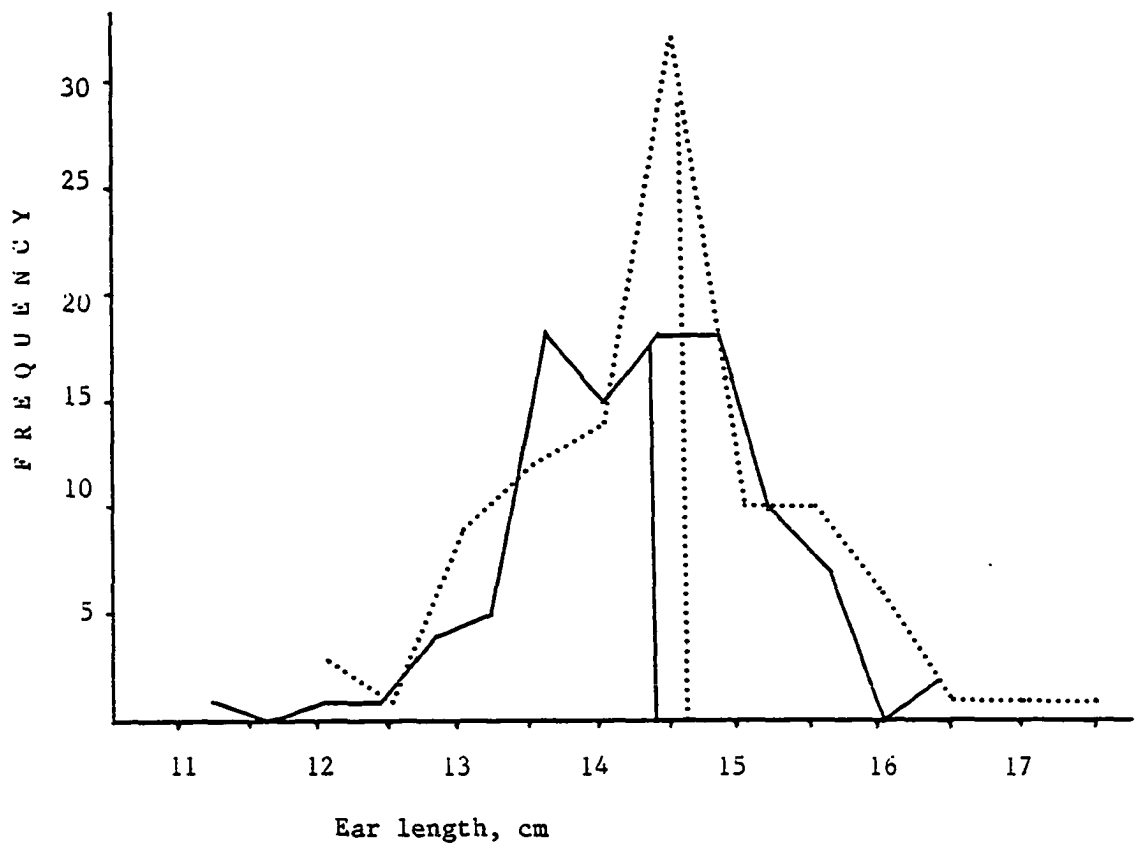

Figure 15. Frequency distributions and means for ear length for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xB84 cross evaluated in four environments

differences between both means were observed for PERTLG, PEDREA, PTAHE, and EARHE. The changes in means were not significant for YIELD, PERTLG, PESTLG, and PEDREA. As in the B73xMo17 single cross, EARHE decreased more than PTAHE: 6.58% VS 5.83%, respectively. The percentages of decreases or increases were less accentuated than those in B73xMo17. No major changes were observed in this single cross for YIELD (Fig. 11), except that the range had an increase toward lower values. EARHE had an increase in range toward lower values (Fig. 13), and the distribution was less peaked in F_2Syn5. Fig. 15 shows that EARLG had an increase in the mean in the F_2Syn5, as well as an increase in range toward higher values. The main change for EARLG occurred for values around the mean; this distribution had a more peaked distribution and both distributions were well differentiated. EARDIM (Fig. 17) had an increase in mean and range and a shift toward higher values. DAYSIL (Fig. 19) had a small decrease in mean in the F_2Syn5 with an increase in range, but both distributions were similar. With regard to minimum values, there were lower values in the F_2 than in the F_2Syn5 for EARLG, ROWNO, COBDIM, and DAYSIL. The advantage for these values in the F_2Syn5 would be for those traits where those values are desirable; that is, PTAHE and EARHE. The F_2Syn5 generation also had better values for EARLG. The maximum values were greater in F_2 than in F_2Syn5 for all traits, except for PESTLG, EARLG, EARDIM, and EARIND. The advantages for F_2Syn5 in these values were for PERTLG, PEDREA, PTAHE, EARHE, EARLG, EARDIM, KERDEP, and YIELD. The ranges were greater in F_2 for PERTLG, PEDREA, PTAHE, ROWNO, and COBDIM.

Table 23. Mean comparisons and normality tests between the F_2 and F_2 Syn 5 for 14 traits in the single cross B73 x B84 evaluated in four environments at Ames (1984, 1985)

Traits	Mean		Diff[a]	Min		Max	
	F_2	F_2 S5		F_2	F_2 S5	F_2	F_2 S5
Root lodging, %	4.94	4.83	-3.33[ns]	0.00	0.00	26.6	14.6
Stalk lodging, %	4.93	5.64	14.40[ns]	0.60	0.57	23.6	26.0
Dropped ears, %	0.24	0.19	-20.83[ns]	0.00	0.00	3.8	2.5
Plant height, cm	185	175	-5.83*	157	142	216	196
Ear height, cm	96	89	-6.58*	75	70	114	110
Ear length, cm	13.9	14.1	1.44*	10.6	11.6	16.0	17.2
Row number, no.	16.6	17.0	2.41*	14.2	14.7	20.5	19.7
Ear diameter, cm	4.37	4.43	1.37*	4.12	4.10	4.68	4.72
Cob diameter, cm	2.79	2.81	0.72*	2.51	2.60	3.06	3.03
Prolificacy, no.	1.05	1.03	-1.90*	0.89	0.77	1.33	1.23
Ear index[f]	0.52	0.51	-1.92*	0.45	0.43	0.56	0.59
Kernel depth, cm	0.79	0.81	2.53*	0.69	0.70	0.92	0.97
Grain yield, kg ha^{-1}	4624	4555	-1.49[ns]	3057	2356	5424	6191
Days to silking, no.	86.6	86.3	0.35*	80.8	81.5	90.3	91.3

[a]Expressed as the superiority of F_2 as compared to F_2 Syn 5 (in percent).

[b]1, 2 indicates F_2 and F_2 Syn 5, respectively.

[c]*, ns indicates significance at 0.05 probability level and nonsignificance, respectively.

[d]* indicates that the test of normality is rejected.

[e]NS indicates that the population is distributed as normal.

[f]Expressed as the ratio of ear height to plant height.

Range		Skewness		Kurtosis		Normality	
F_2	F_2 S5	F_2	F_2 S5	F_2	F_2 S5	1[b]	2[b]
26.6	14.6	1.84	1.60	3.82	2.72	*[d]	*
23.0	25.5	2.07	1.74	8.24	3.46	*	*
3.8	2.5	4.30	2.93	23.5	10.40	*	*
59	54	-0.02	-0.18	0.32	0.25	NS[e]	NS
39	40	0.05	0.07	0.07	-0.28	NS	NS
5.4	5.7	-0.43	0.13	1.37	0.74	NS	NS
6.3	5.0	0.71	0.20	0.71	-0.47	NS	NS
0.56	0.62	0.50	-0.05	0.38	-0.35	NS	NS
0.55	0.44	0.14	-0.03	0.21	-0.18	*	NS
0.44	0.46	0.80	-0.21	1.20	0.49	*	NS
0.12	0.16	-0.35	-0.30	0.06	0.50	NS	NS
0.23	0.27	0.15	0.29	-0.24	0.11	NS	NS
3752	3835	0.07	-0.47	2.01	0.69	NS	*
9.5	9.8	-0.24	0.05	0.14	0.15	NS	NS

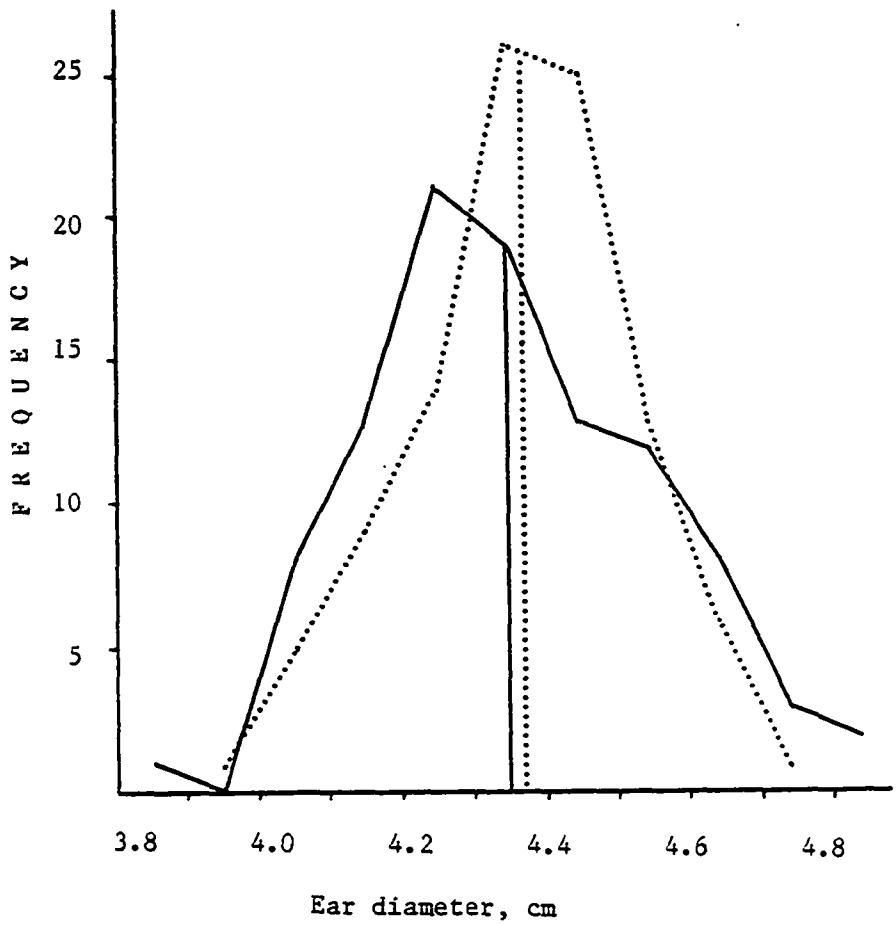

Figure 16. Frequency distributions and means for ear diameter for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xMo17 cross evaluated in four environments

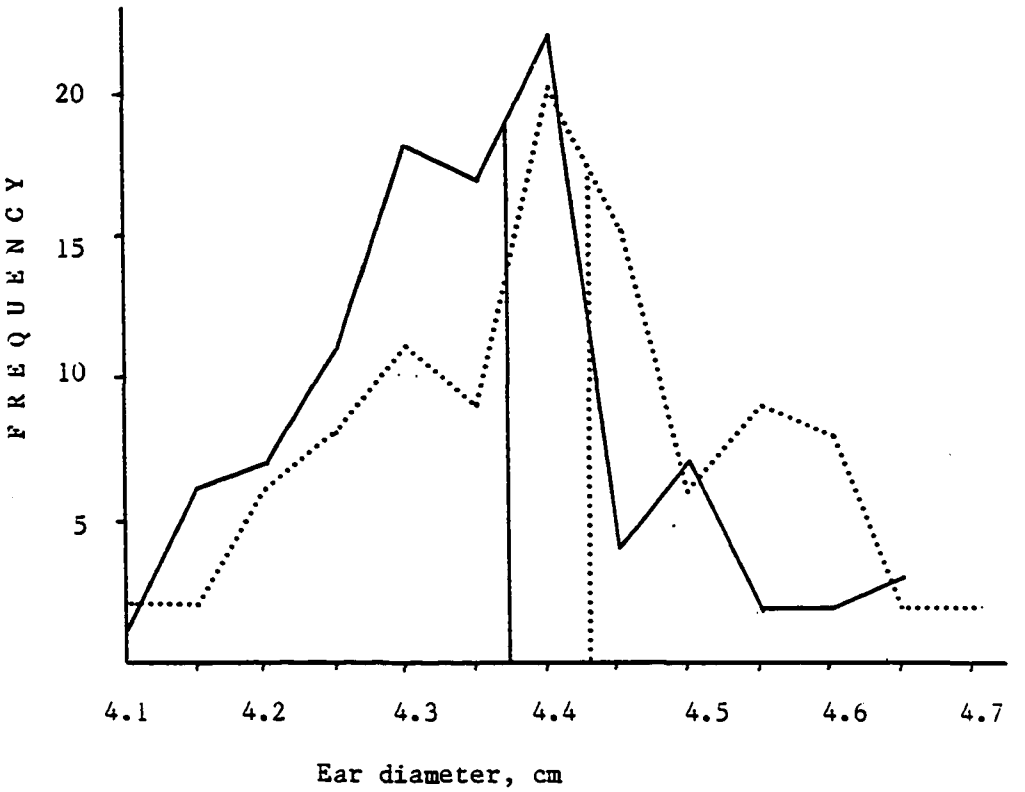

Figure 17. Frequency distributions and means for ear diameter for 100 S_1 progenies for the F_2(___) and F_2Syn5 (...) populations from the B73xB84 cross evaluated in four environments

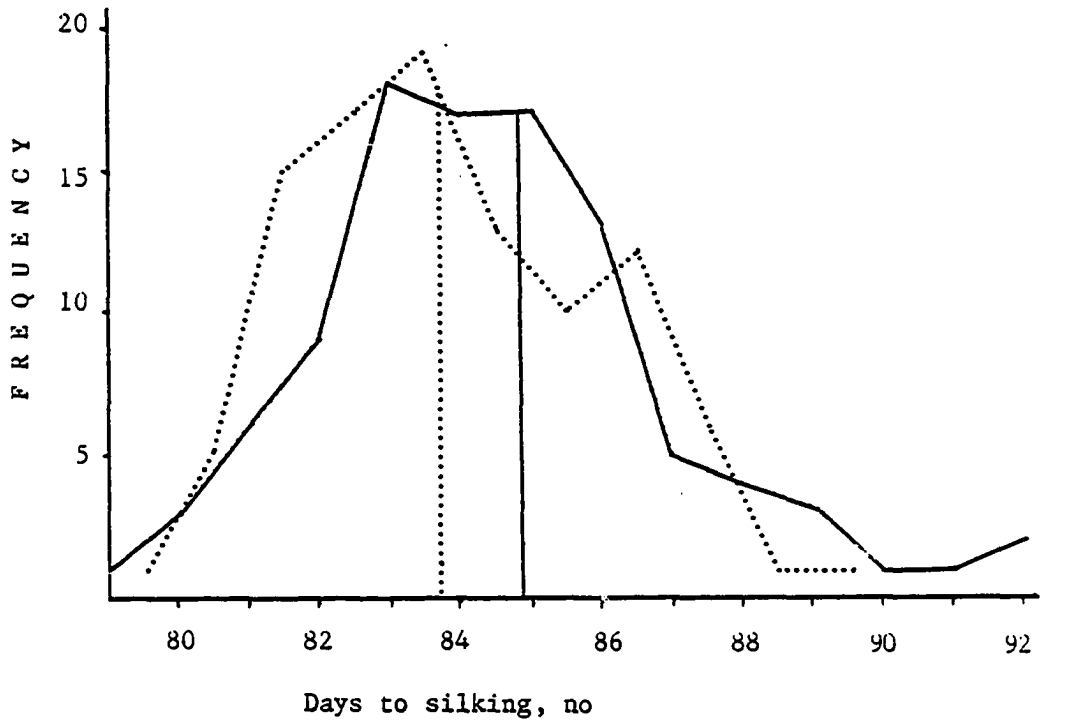

Figure 18. Frequency distributions and means for days to silking for 100 S_1 progenies for the F_2(___) and F_2Syn5(...) populations from the B73xMo17 cross evaluated in four environments

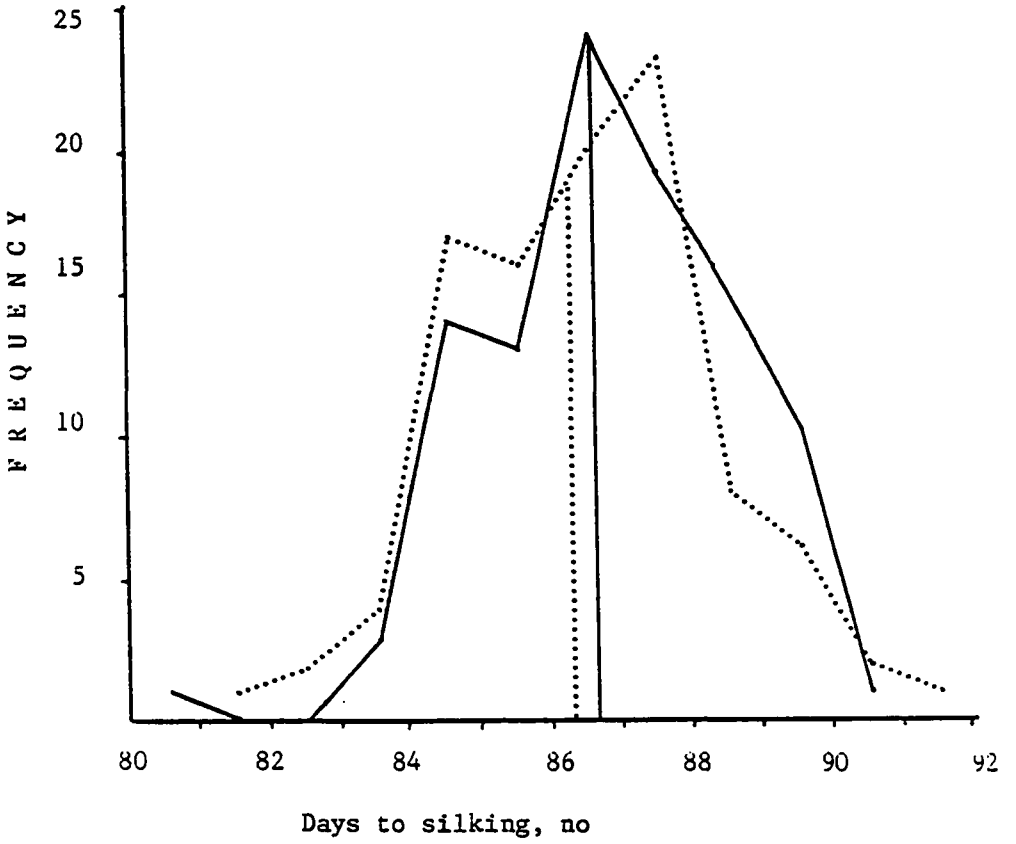

Figure 19. Frequency distributions and means for days to silking for 100 S_1 progenies for the F_2(___) and F_2Syn5(...) populations from the B73xB84 cross evaluated in four environments

Ten of 14 ranges were favorable in the F_2Syn5; therefore, random mating was effective in this F_2 population because the S_1 progenies had greater ranges and more favorable values for most of the traits.

The distribution for PEDREA was more positively skewed and highly peaked in the F_2 than in the F_2Syn5. For PROLIF, the F_2 was more positively skewed and more peaked than its counterpart F_2Syn5. The test of normality was rejected for PERTLG, PESTLG, and PEDREA in both populations, and it was rejected in the F_2 generation for COBDIM and PROLIF and in the F_2Syn5 generation for YIELD.

Some traits exhibited higher transgressive segregates than others. A few favorable recombinations occurred in some populations, and they were in higher frequency in B73xMo17. Alleles for higher yield and other favorable traits were obtained in (B73xB84)F_2Syn5. There were some decreases in ranges for some traits, but the frequency of favorable values were increased in other traits.

DISCUSSION

Mean Analyses with Random Mating

Most of the studies conducted to determine the relative importance of the additive genetic variance in the expression of agronomic traits concluded that most of the variation in corn can be explained by additive effects (Robinson et al., 1955; Gardner, 1963; Robinson, 1963; Hallauer and Miranda, 1981). It is not expected, therefore, that random mating will change the population mean (Hanson and Hayman, 1963; Miller and Rawlings, 1967; Meredith and Bridge, 1971; Altman and Busch, 1984). In this study, there were small increases in the grain yield of B73xMo17 and B73xB84 and small decreases in B77xMo17 and B73xB79 with six generations of random mating (Table 9). The changes, however, were not significant as measured by the regression coefficients. Changes in allele frequency are not expected with random mating (Falconer, 1981), unless some changes had occurred due to natural selection or inadvertent selection. Each generation of random mating was produced under different environments; some genotypes could have been favored unintentionally at pollination, at the thinning stage, or during growth. The results for the four single crosses are similar to those reported by Miller and Rawlings (1967) and by Meredith and Bridge (1971) in cotton.

Epistasis involving linkage could affect differentially the means of the populations with random mating. There is evidence of epistasis in single crosses of corn (Hallauer and Miranda, 1981). Negative epistasis may have been present in B77xMo17, where a disruption of favor-

able gene interactions for yield may have caused a 1.95% decrease in yield after six generations of random mating.

The random mating generations of B73xB84 and B73xB79 did not differ in grain yield as measured by their regression coefficients. Because none of the regression coefficients was significantly different from zero, the results are in agreement with those reported by Altman and Busch (1984), and the small changes can be attributed to sampling errors. It does not seem that the shifts observed in some of the means for yield were attributed to random genetic drift because the sample size was adequate, according to the results of Baker (1968).

Grain moisture (MOIST) was reduced for the four single crosses. Two of them (B73xMo17 and B73xB79) were significantly different from zero. Some changes occurred because of random mating that can be attributed to either natural selection, because each generation was produced in different years, or epistatic effects. When the contribution of each locus in one metric trait is independent of all other loci, the presence of linkage cannot modify the expected results for the mean. But if some interactions exist, the effect of linkage should be noted as an increase of those effects in that trait (Falconer, 1981). Therefore, epistasis cannot be excluded as an explanation for the changes in grain moisture with random mating.

Theoretically, the changes in means can be explained by a one locus model with two alleles. Any changes in means can be attributed to either a change in allele frequency and by a change in the dominance effects through the generations of random mating. The changes in means

when epistasis and linkage disequilibrium are present can be explained by a two-locus model with two alleles each. The mean changes would depend upon the amount of genetic disequilibrium and the relative importance of epistatic effects; these changes are expected to be higher in those crosses formed with nonrelated parents.

To show the effects of epistasis on means when there is no gametic phase equilibrium and epistasis, let there be alleles $A_1, \ldots, A_{k1}$ at locus 1 and alleles $B_1, \ldots, B_{k2}$ at locus 2. At loci 1 and 2, the array of alleles is: $\Sigma_i\ p_iA_i,\ \Sigma_i\ q_kB_k$. If we have a random mating population in gametic disequilibrium,

$p_i = P(A_i),\quad q_i = P(B_i)$.

The probability that a gamete is generated is:

$P(A_iB_j) = p_iq_k + D_{ik} = P(A_iB_j$ gamete)

= product of their respective allele frequency (p_iq_k) plus an amount of disequilibrium (D_{ik}) generated among the two alleles. Also

$\Sigma_k\ P_{ik} = p_i + \Sigma_k\ D_{ik} = P(A_i) = \Sigma_k\ D_{ik} = 0$, and

$\Sigma_i\ P_{ik} = q_k + \Sigma_i\ D_{ik} = P(B_k) = \Sigma_i\ D_{ik} = 0$.

If we have the reference population

$(\Sigma_i\Sigma_j\ p_ip_jA_iA_j)\ (\Sigma_k\Sigma_l\ q_kq_lB_kB_l)$

and if we random mate this population, the array of the offspring generation is

$$\{\Sigma_i\Sigma_k\ (p_iq_k + D_{ik})A_iB_k\}\ \{\Sigma_j\Sigma_l\ p_jq_l + D_{jl})A_jB_l\}$$

$$= \Sigma_i\Sigma_j\Sigma_k\Sigma_l\ (p_iq_k + D_{ik})(p_jq_l + D_{jl})A_iB_k\ /\ A_jB_l.$$

Define the genotypic value of an individual Y_{ijkl} with respect to the reference population as:

Y_{ijkl} = the genotypic value of $A_iA_jB_kB_l$

$$= Y.... + \alpha_i^1 + \alpha_j^1 + d_{ij}^1 + \alpha_k^2 + \alpha_l^2 + d_{kl}^2 + (\alpha^1\alpha^2)_{ik}$$
$$+ (\alpha^1\alpha^2)_{il} + (\alpha^1\alpha^2)_{jk} + (\alpha^1\alpha^2)_{jl} + (\alpha^1 d^2)_{ikl} + (\alpha^1 d^2)_{jkl}$$
$$+ (d^1\alpha^2)_{ijk} + (d^1\alpha^2)_{ijl} + (d^1 d^2)_{ijkl},$$

where Y.... = the mean, and is defined as:

$\Sigma_i\Sigma_j\Sigma_k\Sigma_l\ p_ip_jq_kq_l(Y_{ijkl})$;

superscript 1 represents locus 1 and superscript 2 represents locus 2;

$\alpha_{i,j,k,l}$ = additive effect of alleles i,j,k,l, respectively;

d_{ij}, d_{kl} = dominance effects of loci 1 and 2, respectively;

$(\alpha^1\alpha^2)$ = additive x additive epistatic effects between alleles as indicated;

$(\alpha^1 d^2)$, $(d^1\alpha^2)$ = additive x dominant epistatic effects; and

$(d^1 d^2)_{ijkl}$ = dominant x dominant epistatic effects between loci 1 and 2.

Therefore, the mean of that population when epistatic effects are considered and with gametic disequilibrium is:

$$\mu = \Sigma_i\Sigma_j\Sigma_k\Sigma_l\ (p_ip_jq_kq_l + D_{ik}p_jp_l + D_{jl}p_iq_k + D_{ik}D_{kl})\ Y_{ijkl}$$

$$= Y.... + \Sigma_i\Sigma_k\Sigma_j\Sigma_l\ D_{ik}p_jq_lY_{ijkl} + \Sigma_i\Sigma_k\Sigma_j\Sigma_l\ D_{jl}p_iq_kY_{ijkl}$$

$$+ \Sigma_i\Sigma_k\Sigma_j\Sigma_l \; D_{ik}D_{jl}Y_{ijkl} \cdot$$

The final derivation relies on the following assumptions:

1) Sums of D's over a single subscript are equal to zero, that is,

$\Sigma_i D_{ik} = \Sigma_k D_{ik} = \Sigma_j D_{jl} = \Sigma_l D_{jl} = 0$; and

2) if the D's do not share both subscripts with the products of main effects or interactions, the result is zero.

Therefore, substituting the value of Y_{ijkl} we have

$$\mu = Y.... + \Sigma_i\Sigma_k \; D_{ik} \left[Y.... + \alpha_i^1 + \alpha_k^2 + (\alpha\alpha)_{ik}^{1\,2} \right]$$

$$+ \Sigma_j\Sigma_l \; D_{jl} \left[Y.... + \alpha_j^1 + \alpha_l^2 + (\alpha\alpha)_{jl}^{1\,2} \right.$$

$$+ \Sigma_i\Sigma_k\Sigma_j\Sigma_l \; D_{ik}D_{jl} \left[Y.... + \alpha_i^1 + \alpha_j^1 + \alpha_k^2 + \alpha_l^2 + d_{ij}^1 + d_{kl}^2 \right.$$

$$+ (\alpha\alpha)_{ik}^{1\,2} + (\alpha\alpha)_{il}^{1\,2} + (\alpha\alpha)_{jk}^{1\,2} + (\alpha\alpha)_{jl}^{1\,2}$$

$$\left. + (\alpha d)_{ikl}^{1\,2} + (\alpha d)_{jkl}^{1\,2} + (d\alpha)_{ijk}^{1\,2} + (d\alpha)_{ijl}^{1\,2} + (d d)_{ijkl}^{1\,2} \right].$$

finally, because of assumptions 1) and 2)

$$\mu = Y.... + \Sigma_i\Sigma_k \; D_{ik}(\alpha\alpha)_{ik}^{1\,2} + \Sigma_j\Sigma_l \; D_{jl}(\alpha\alpha)_{jl}^{1\,2}$$

$$+ \Sigma_i\Sigma_k\Sigma_j\Sigma_l \; D_{ik}D_{jl}(d d)_{ijkl}^{1\,2} \cdot$$

Thus, we can show that in the absence of epistatic effects the mean is not affected by gametic equilibrium; that is,

$$\mu = Y.... + \Sigma_i\Sigma_k \; D_{ik}(Y.... + \alpha_i^1 + \alpha_k^2) + \Sigma_j\Sigma_l \; D_{jl}(Y.... + \alpha_j^1 + \alpha_l^2)$$

$$+ \Sigma_i\Sigma_k\Sigma_j\Sigma_l \; D_{ik}D_{jl}(Y.... + \alpha_i^1 + \alpha_j^1 + \alpha_k^2 + \alpha_l^2 + d_{ij}^1 + d_{kl}^2)$$

$= Y.... + 0$ because of assumtions 1) amd 2) (Cockerham, 1954;

Weir and Cockerham, 1979).

Fluctuations in STAND were significant among the generations of random mating. The variation was not at random, and may have been caused by genetic differences in viability of some entries.

The percentages of root and stalk lodging and dropped ears had significant interactions with environments. These traits are affected by environment and are difficult to estimate because the environmental conditions were neither adequate nor uniform for the sites in which the experiments were conducted. Therefore, it is difficult to make conclusions about the differential performance of the generations of random mating. Another difficulty is that the distributions of these traits were not normal. B73xB79 and B77xMo17 were more resistant to root lodging and more susceptible to stalk lodging than were B73xMo17 and B73xB84.

B73xB84, the related line cross, did not show any significant shifts in YIELD and MOIST. Some significant shifts did occur in the crosses between the intermediate and most unrelated parents. If no shift occurred in the cross of related parents, natural selection was not an important factor in the generations of random mating. Natural selection could have played a different role in B73xMo17 and B73xB79 because these populations have greater variability than did B73xB84. Comstock and Robinson (1952) postulated that natural selection could be the source of significant changes in allele frequency over a period of several generations.

Some of the differences in means could be attributed to the vari-

ation in the number of plants in different environments. The greatest variation in stands occurred for (B73xMo17)F_2Syn2 and (B73xB84)F_2Syn3, which had lower STANDS (about five plants less than the average for that cross). If we analyze STANDS by environment, three environments had significant differences in STAND among generations; that is, the variation was not random, but generated by either natural selection or through recombination, where some traits related to viability were affected. According to the results reported by Humphrey et al. (1969), they estimated that recombination can lead to chromosomal segments less fit than those of their parents, giving rise to a population less fit than the parents.

The F_1 generations for all single crosses were statistically different from their F_2 generation, except for B73xB84. This difference was expected because of the assumption that inbreeding depression is related to the presence of some dominance effects and differences in gene frequency (Falconer, 1981; Hallauer and Miranda, 1981). Based on the pedigree of the lines included in the crosses, B73xMo17, due to its high heterotic pattern, should show the greatest inbreeding depression and B73xB84 the least.

Evidence that some breakup of linkage blocks did occur was observed in the differential performance in two of the single crosses. B73xMo17 had a slight increase in YIELD, but MOIST decreased significantly; that is, more yield was obtained as the grain moisture decreased. In B73xB79, the effect was different; YIELD decreased 1.96% per generation of random mating, but, at the same time, MOIST was re-

duced significantly. Mean performance was not affected in a consistent manner. Environmental factors could have influenced the small differences in some traits because the genetic potential could not be expressed in some entries due to the unfavorable conditions; i.e., the 1984 conditions and the results at Ankeny in 1985.

Analyses of Variability

Analyses of the S_1 progenies from the F_2 and F_2Syn5 populations were different for the two single crosses. There were significant differences among S_1 lines within each population before and after random mating. There also was some evidence that five generations of random mating were enough to produce genetic differences through recombination in the populations that were reflected in the S_1 progenies derived upon those populations. The most noticeable difference was the significant contrast of F_2 VS F_2Syn5 in B73xMo17. The significant difference for the F_2 VS F_2Syn5 comparison suggests recombination had separated the populations genetically after five generations of random mating. New genetic combinations were created, and these new forms reacted in a different way to the same environmental conditions than the original populations. Genotypes after five generations of random mating were different at least in some gene sequences and in the relationship among some traits. The same phenomenon was observed in B73xB84, where only three traits did not change significantly before and after random mating. There were no changes for PEDREA in both single crosses; variation among S_1 progenies was small for PEDREA for

the environments in which they were evaluated.

Pooling all the progenies for both crosses, the contrast F_2 VS F_2Syn5 was significant for most traits, suggesting that the F_2 generations were different than their respective F_2Syn5; random mating, therefore, was effective in changing the genetic arrangement of those populations. These results are similar to those published by Miller and Rawlings (1967) and by Meredith and Bridge (1971) in cotton. A computer simulation study reported by Baker (1968) suggested that random mating was effective in causing recombination within populations. Altman and Busch (1984), however, did not find random mating F_2 populations was effective for increasing genetic variability in wheat. If variability in YIELD changes, those changes observed in other traits correlated with YIELD were an effect of correlated response and cannot be attributed to the effects of random mating.

The mean contrast (B73xMo17)F_2 VS (B73xB84)F_2 and (B73xMo17)F_2Syn5 VS (B73xB84)F_2Syn5 was significant for all traits. The differences in mean performance were expected due to the genetic differences between the single crosses.

The F_1 of the cross of two homozygous parents is a highly heterozygous population; the F_2 population obtained from this F_1 is a population in linkage disequilibrium for loci with recombination values less than 0.5 (Cockerham, 1963). The S_1 progenies had G x E interactions for only a few traits. The F_2Syn5 S_1 progenies tended to interact more with environments than did the F_2 because heterozygosity is expected to be higher in the F_2 and the environmental variance appears to

be related to the degree of heterozygosity (Robertson and Reeve 1952; Matzinger, 1963). Gene and genotypic frequencies among generations of populations will not change in the absence of selection, migration, and mutation (Falconer, 1981). Migration should not have caused a signficant change because 250 plant samples were included for each generation of random mating. Mutation could have occurred, but the expression of mutation would be negated by random mating. Selection and genetic disequilibrium could have contributed to the changes in the heterozygote frequencies. These changes also could contribute to the higher G x E interaction in F_2Syn5.

Genetic Variance Estimates

Comstock and Robinson (1952) indicated the assumptions involved in the derivation of the expected mean squares:

1. Random choice of individuals mated for the production of S_1 progenies.

2. Random distribution of genotypes in the environments.

The assumptions that have to be met for the genetic interpretation of the variance components (Comstock and Robinson, 1952) are:

1. Regular diploid behavior at meiosis.

2. Population gene frequency = 0.5 at all loci where segregation occurs.

3. No multiple alleles.

4. No maternal effects.

5. No correlation of genotypes at segregating loci; that is, no

linkage among genes affecting the characters studied, or, if this exists, the distribution of genotypes is at equilibrium with respect to coupling and repulsion phase linkages.

6. No epistasis.

The second assumption is fulfilled because of the F_2 generation from the cross of two homozygous lines. In the F_2Syn5 some deviations due to natural selection cannot be avoided through the generations of random mating. Inadvertent selection could be the source of significant changes in allele frequency over generation of random mating.

Multiple alleles in the F_2 of homozygous lines are not frequent (Comstock and Robinson, 1952). Maternal effects usually have not been important in corn.

The problem arises with assumption 5 for characters influenced by many genes. In the F_2 generation of the cross of two homozygous parents, linkage equilibrium is not expected for loci with recombination values less than 0.5 (Comstock and Robinson, 1952; Cockerham, 1963). This assumption, however, could be approximated in the F_2Syn5, except for those genes linked very tightly (Robinson et al., 1949). On the other hand, Anderson (1939) postulated that linkage will hinder recombination in species crosses when a large number of genes is involved.

Most reports in corn suggest epistasis is not very important in most corn populations. Comstock and Robinson (1948, 1952) reported that epistasis causes an upward bias in the estimation of the average degree of dominance. Epistasis also affects our estimates of heritability on a S_1 progeny mean basis but the bias cannot be large.

The genetic variance in B73xMo17 increased from F_2 to F_2Syn5 for PESTLG, EARHE, EARIND, and PROLIF, as measured by the comparison of the difference in the variance estimates. If the difference was greater than the sum of their respective standard errors, that difference was considered as significant. This is an approximation because we do not have a reliable test to use for testing the significance in the change in variances. Those shifts were significant only for EARIND and PROLIF, suggesting that the predominant linkage phase for those traits was repulsion (Robinson et al., 1960; Hanson and Hayman, 1963; Baker, 1968, 1984; Meredith and Bridge, 1971; Hallauer and Miranda, 1981). Estimates of genetic variance decreased for PERTLG, PEDREA, EARLG, EARDIM, COBDIM, ROWNO, YIELD, and DAYSIL, suggesting that coupling linkage phases were predominant in these traits. These shifts were significant for PEDREA, EARDIM, COBDIM, ROWNO, and DAYSIL, but it was not significant for YIELD. These results agree with the simulation studies reported by Bos (1977) and Pederson (1974) who reported that random mating would not be effective in increasing the range of the genotypic variance if the predominant linkage phase was coupling.

An increase in the genetic variance estimates in B73xB84 from F_2 to F_2Syn5 was observed for PERTLG, PESTLG, EARHE, EARLG, EARDIM, EARIND, PROLIF, KERDEP, YIELD, and DAYSIL. The changes were significant for PESTLG, EARLG, EARIND, PROLIF, KERDEP, and YIELD, suggesting that repulsion phase linkages were predominant for these traits. Coupling phase linkage was suggested for PEDREA because of a significant reduction in the genetic variance estimate. These results agree with the

expectations reported by Baker (1968), and with the results published by Miller and Rawlings (1967), and Meredith and Bridge (1971) in cotton, where an increase in the range of genetic variance was observed under random mating.

Significant changes in the estimates of genetic variances from F_2 to F_2Syn5 are confounded if dominance variance is important, because the genetic variance estimate of S_1 progenies includes 1/4 of dominance variance and the dominance variance is always biased upward, irrespective of the predominant linkage phase. The dominance variation will be reduced with random mating. Robinson et al. (1949) and Gardner and Lonnquist (1959) observed a consistent and appreciable reduction in dominance variance in advanced generations of random mating. Robinson et al. (1949) reported also a reduction in the estimates of additive genetic variance in the F_8 as compared to the F_2.

These results showed that 10 of 14 shifts in genetic variances in B73xMo17 were considered as due to coupling, and 10 of 14 shifts were considered as due to repulsion in B73xB84. A possible explanation for the differences is that, with related parents, most of the genes are the same, except for small differences in some alleles for which both parents differ. For the related-line cross, they complement each other in the following manner. Consider a digenic model with two loci: Ab/aB, where A came from the first parent, while B came from the other parent. In this way, the interaction would result in repulsion linkage phase. When the parents have a greater difference, as the case for B73xMo17, one possible explanation is that the linkage phase was coupling; that

is, each parent contributed a block of genes for a trait and the F_1 combined the contribution from each parent in blocks. Each parent has specific favorable linkage blocks; i.e., ABCdef/abcDEF, where the block ABC came from one parent and block DEF from the other parent, and in this way, we will have coupling. Blocks of positive alleles in one parent are complemented with another positive block from the other parent. The results suggested that recombination was enhanced as measured by the shifts in genetic variances from the F_2 to the F_2Syn5. The changes in genetic variances reflected either changes in linkage disequilibrium or changes in allele frequency, which occurred during the successive generations of random mating, as was postulated by Miller and Rawlings (1967).

An increase in the genotypic range of populations subjected to random mating was not always observed, as it was postulated by Baker (1968). In most instances, the random mated populations differed in the distributions of the S_1 progeny means. But, as was emphasized by Hanson and Hayman (1963) and by Baker (1968), the range of the genetic variability cannot be increased, and the beneficial effects will be observed after the inclusion of some recurrent selection.

Yield and three yield components had different predominant linkage phases. This suggests that each trait was controlled by independent systems, and pleiotropism can be excluded as the source of correlation among those traits. The trend in the changes of genetic variances would be expected to be in the same direction. If no reduction or increase in genetic variance occurred with random mating, this does not

exclude the presence of linkage disequilibrium, because linkage alone can hinder recombination (Anderson, 1939), so these traits could be held in tight linkage.

The estimates of genetic variances among individual experiments were not consistent for YIELD. The estimates of genetic variances from F_2 to F_2Syn5 decreased in 1984 (environments 1 and 2), suggesting coupling phase, but the estimates increased in 1985 (environments 3 and 4), suggesting repulsion phase linkage. The explanation can be attributed to the effects of environments that voided the complete expression of the genetic potential of some progenies. The estimates of genetic variance were reduced in unfavorable environments and contributed the conflicting results of the real genetic situation. The main problem with the interpretation of genetic variances in individual experiments is that those estimates are confounded with the GxE interaction.

To determine how the bias in the estimation of genetic variances can occur, Falconer (1981) presented some possible explanations. The results presented showed that linkage or gametic phase disequilibrium is an additional source of genetic variance; these effects were present when the genotypic frequencies at two or more loci for a metric trait were not what would be expected from their allele frequencies. These effects can be represented as a matrix, where the variances for each locus are those values in the diagonal, and the elements off the diagonal represents the correlations between pairs of loci that interact. Under linkage equilibrium, all off-diagonal elements would be

zero; i.e., no interaction among loci. When repulsion phase was assumed to predominate, loci with favorable effects were linked with loci with unfavorable effects (Ab/aB); thus, their genetic covariance was expected to be negative, and the additive genetic variance was underestimated. When coupling phase was assumed to predominate, loci with favorable effects were linked (AB/ab), and their genetic covariance was expected to be positive, leading to an overestimation of the additive genetic variance. But if linkage phase was balanced between repulsion and coupling, there would be no bias present, and the additive genetic variance was estimated without bias. Some traits did not show a significant shift in the genetic variance estimates from the F_2 to F_2Syn5; in these instances, we can not rule out the presence of linked loci. The actual bias would depend on the amount of linkage and the relative prevalence of coupling and repulsion linkage phases (Comstock and Robinson, 1952).

Most of the G x E interaction estimates were not significant, but the F_2Syn5 tended to interact more with environments than did the F_2. The F_2s were possibly more heterozygous than the F_2Syn5s, because some segregation occurred due to the breakup of gene-linkage blocks. Thus, if allele frequency is unchanged, the genotypic frequency can change toward their equilibrium value if we assume that the F_2 has an excess of heterozygotes. The genotypic frequency is expected to change under random mating toward the genotypic frequency of equilibrium.

The estimates of phenotypic variances showed the same trend in both populations as those observed for estimates of genetic variances.

Because most of the variation observed was genetic and the GxE interactions were of little significance, these estimates also tended to be greater in F_2Syn5. The error variances were very consistent among populations.

Heritability Estimates

Heritability was estimated as σ^2g/σ^2ph. With the use of S_1 lines, the expected component of variance of S_1 lines is equal to $\sigma^2A + 1/4\ \sigma^2D$. For those traits where epistatic effects were of importance, we need to add an extra term (σ^2I). All heritability estimates were overestimated, depending on the bias due to the amount and phase of linkage and the relative importance of dominance and epistatic effects. This is a broad sense heritability estimate based on S_1 line means. We expect that dominance will be more important in those crosses expressing high heterosis, such as B73xMo17, and less important in B73xB84. If linkage is present, the estimates of σ^2D for the F_2 will have greater bias than the F_2Syn5 because dominance variance is biased positively regardless of the linkage phases.

Most of the heritability estimates for the same trait were higher in B73xMo17 populations than in B73xB84 populations. Because the dominance variance was assumed to be higher in the B73xMo17 population, the estimates of genetic variance in B73xMo17 may have had a greater bias due to linkage than those in B73xB84.

EARHE, PTAHE, ROWNO, and DAYSIL had the highest heritability estimates in both single crosses, which suggests these traits were con-

trolled by a relatively low gene number and, therefore, less affected by environmental effects. The heritability estimate for YIELD in F_2Syn5 was 10.5% smaller, compared with the F_2 in B73xMo17, which was attributed to the higher GxE interaction for the F_2Syn5. Heritability estimates increased in F_2Syn5 in B73xB84 because of an increase in the estimate of genetic variance after random mating. The increase in the phenotypic variance in this cross was due to an increase in the genetic variance because GxE interaction decreased slightly.

The estimates for the genetic coefficient of variation for YIELD showed that the variability for F_2Syn5 was 3.9% less, compared with F_2 in B73xMo17, but increased 24.8% for the F_2 in B73xB84, because a reduction in both the genetic variance and mean in B73xMo17 populations, and to an increase in the genetic variance in B73xB84 populations. The effects of random mating were more favorable in B73xB84 where some favorable recombinants gave rise to better genotypes. In B73xMo17, because of its high performance, the favorable combinations were not produced; that is, the favorable combinations in B73xMo17 were in lower proportion, as compared to B73xB84. Because repulsion phase linkage was expected to be higher in B73xMo17, this factor may have hindered recombination, as it was postulated by Anderson (1939) and demonstrated by Gates et al. (1957). Some favorable alleles in coupling were recombined in B73xMo17, resulting in some genotypes that were inferior to those from which they were derived. According to this parameter, EARHE, PTAHE, and PROLIF were favored with random mating in both single crosses, because the estimates of variance among S_1 lines showed an

increase in the variability for those traits. The decrease in COBDIM was considered as favorable in both single crosses. EARLG, EARDIM, KERDEP, and DAYSIL had opposite changes in both single cross populations; decreased with random mating in B73xMo17 and increased in B73xB84. The genetic coefficients of variation were of greater magnitude in B73xMo17 than in B73xB84 because of its greater genetic variability.

Genetic and Phenotypic Correlations

Miller and Rawlings (1967) pointed out that when the loci that affect a trait are not in linkage equilibrium, it was expected that the genetic correlations were going to move toward the equilibrium value with random mating. In B73xMo17, 28 out of 91 genetic correlation coefficients did not change between the F_2 and F_2Syn5 generations. Significant changes in trait associations occurred between the correlations from F_2 to F_2Syn5 in 19 out of 91 (20.9%) pairs of genetic correlations; YIELD was involved in six of the 19 estimates. An increase in the genetic correlation coefficients was observed in 13 of 19 (68%), which suggests that the predominant linkage phase was repulsion. Similar results were reported by Miller and Rawlings (1967) and by Meredith and Bridge (1971). The association of YIELD with three yield components was observed to decrease significantly only for YIELD - KERDEP. EARIND had greater correlations with EARHE and PTAHE, which suggests that selection for EARHE could be based on an index (ear position), (Rivera Gomez et al., 1972).

In B73xB84, 10 of 91 (9.9%) significant genetic correlation shifts occurred from F_2 to F_2Syn5. There were some other changes in the relation among some pairs of traits, but they were not significant. An increase in the genetic correlation coefficient was observed in 6 of 10 (60%) trait associations. No changes were observed in the associations between YIELD and all other traits. No changes in the genetic correlations suggest they were near an equilibrium value, assuming high proportions of additive genetic variance (Hanson and Hayman, 1963). The changes in the genetic relations among some pairs of traits suggest that the breakup of linkage blocks was promoted by random mating. One of the objectives of random mating was fulfilled in the sense that recombination between linked genes has been favored, twice the proportion in B73xMo17 as that of B73xB84. Correlation coefficients are due to the correlation of breeding values (Falconer, 1981), but because the data used to obtain these correlations include some dominance effects and possibly some epistatic effects, these correlations should be considered with caution. According to Mode and Robinson (1959), these coefficients are biased. The bias is expected to be higher in the F_2 generation. Finally, the estimates of genetic correlations are not precise because they are subject to large sampling errors.

The phenotypic correlations include as causes of correlation those due to genetic effects as well as those due to environmental effects (Falconer, 1981). There were 15 of 91 (16.6%) significant shifts from F_2 to F_2Syn5 in B73xMo17 and 13.2% in B73xB84. YIELD was involved in

5.5% of the significant shifts in B73x Mo17 and only 1.1% in B73xB84. An increase in the phenotypic correlation was observed in 11 of 15 (73%) shifts in B73xMo17, while 7 of 12 (58%) shifts were observed in B73xB84. In B73xB84, the phenotypic correlations were enhanced slightly for most of the associations with YIELD except that for PEDREA, which was significantly reduced from positive in F_2 to negative in F_2Syn5. Higher proportion of shifts were observed in B73xMo17. This was expected because, in this cross, the genetic constitution of the inbred parents was different.

There has been evidence that recombination was promoted by random mating, as indicated by Hanson (1959a,b), Hanson and Hayman (1963), Baker (1968, 1984), Miller and Rawlings (1967), Meredith and Bridge (1971), and Humphrey et al. (1969). According to some theory, linked genetic disequilibrium is expected in B73xMo17. This was corroborated in this study because the highest frequency of significant shifts in genetic and phenotypic correlations were observed in B73xMo17. The greatest significant shifts for YIELD were observed in the B73xMo17 cross.

S_1 Mean Analyses among Populations

Most of the traits showed a decrease in their means from the F_2 to the F_2Syn5 generations after random mating as measured by the 100 S_1 progeny means. Most of the changes were significant. The changes in YIELD, PERTLG, PESTLG, and PEDREA were not significant in B73xB84. There was a trend in B73xMo17 to have more negative shifts from F_2 to

F_2Syn5 than in B73xB84. These differences in performance of the S_1 progenies can be attributed to the effects of inbreeding depression, which was expected to be higher in B73xMo17 because of possible dominance and epistatic effects. The changes in means of S_1 progenies of B73xMo17 did not seem to be proportional to the dominance and inbreeding; thus, some epistatic interactions were possible causes because the level of inbreeding is the same in both generations (S_1 = 0.5) and the dominance effects were of less importance in the F_2Syn5 generation. Epistasis cannot be ignored, and the shifts in means may be attributed to epistatic effects. The B73xMo17 single cross was expected to show more epistatic effects than B73xB84. The high heterosis manifested in the F_1 of this cross cannot be explained by dominance itself.

PESTLG, PTAHE, EARHE, EARLG, COBDIM, EARIND, PROLIF, and YIELD means decreased from F_2 to F_2Syn5 in B73xMo17. This result is favorable for selection in PESTLG, PTAHE, EARHE, and COBDIM because lower values for those traits are desirable. Thus, random mating was effective in creating some variation not observed in F_2. The ranges, however, were not increased in the F_2Syn5; this result was expected, as it was postulated by Hanson and Hayman (1963). They explained that the approach to the idealized genotype will be achieved only through some recurrent selection program. According to Falconer (1981), the mean under inbreeding tends to change as a consequence of dominance at the loci concerned with a trait, and that the direction of the change is toward the value of the more recessive alleles. Thus, we should expect greater inbreeding depression in the F_2, but this was not observed be-

cause the F_1 was not included in these trials and the estimate of inbreeding depression was based on the means of the S_1 progenies.

There was a trend in both single crosses for the mean of S_1 progenies to decrease from the F_2 to the F_2Syn5 generation. The F_2 is a population in disequilibrium when it represents the generation of the cross of two inbreds that are not related. The F_2Syn5 generation will approach genetic equilibrium, depending on how the approach to equilibrium is achieved; that is, how tight the linkages and how important are the dominance effects. The only differences between the F_2 and F_2Syn5 populations are attributed to the differences in the genotypic constitution of both populations.

The mean of a population with inbreeding and taking the combined effects of all the loci that affects a trait is (Falconer, 1981):

$$M_F = \sum a(p - q) + 2(\sum dpq)(1 - F)$$

$$= M_o - 2 F \sum dpq \quad ,$$

where

M_o = the original mean without inbreeding,

p, q = gene frequencies for the favorable and unfavorable alleles, respectively,

a = genotypic value, and

d = dominance effect.

This expression shows that the mean for a trait is going to suffer a decrease in a rate proportional to the inbreeding level if loci combine additively. If there is epistasis, that relation is not linear; as F increases, inbreeding depression also increases if the epistatic

effects are favorable on the average and the rate decreases if they are unfavorable. In this study, the F_2 and F_2Syn5 were exposed to the same inbreeding depression, as measured by the S_1 progeny means. The only difference expected between both populations is epistatic effects in the F_2. Then:

$$M_F = M_o - 2\,(0.5)\,\Sigma\, dpq\ .$$

Assuming p=q=0.5, and complete dominance, the reduction expected for a pair of genes would be 0.25. If we want to calculate the reduction expected, we multiply by the number of genes that control any trait. If we assume that yield is controlled by 2000 pairs of genes, the reduction expected would be about 500. But if epistasis is important we expect a higher reduction in F_2 rather than in F_2Syn5, because after generations of random mating, epistasis will be dissipated and dominance effects would decrease under linkage effects. In this study, there was a decrease in S_1 mean traits in F_2Syn5 as compared to S_1 means of the F_2. The possible explanation is that the epistatic effects were negative on the average in F_2 and positive in F_2Syn5. The other alternative is a small change in allele frequency during the generations of random mating, and this change would explain the decrease in yield.

SUMMARY AND CONCLUSIONS

The effects of six generations of random mating were evaluated in four single crosses of maize: B73xMo17, a cross of two unrelated parents; B73xB84, a cross of two related parents; and B73xB79 and B73xMo17, crosses of lines with intermediate relation. Six generations of random mating in each single cross were evaluated in six environments in 1984 and 1985. The objective of these trials was to estimate the change in means over generations of random mating. Additionally, 100 S_1 progenies were derived from the F_2 and F_2Syn5 generations of B73xMo17 and B73xB84. The S_1 progenies were evaluated to estimate the changes in genetic variances by random mating. Data were recorded for grain yield, ear height, ear length, ear diameter, ear height, plant height, stalk lodging, root lodging, dropped ears, prolificacy, kernel depth, cob diameter, ear index, and days to silking.

Analyses of the different generations of random mating showed a small increase in grain yield of B73xMo17; however, these changes were not significant, as measured by their regression coefficients. There were significant decreases for grain moisture in B73xMo17 and B73xB79. Changes in gene frequency are not expected to occur with random mating (Falconer, 1981). In this study, those changes were attributed either to natural selection because each generation was produced under a different environment or to epistatic effects that could be important in the crosses composed by less related parents. It was shown that the mean is affected by gametic disequilibrium only when epistasis is pre-

sent.

The means of the F_2 and F_2Syn5 generations were statistically significant for B73xMo17 and B73xB84; therefore, random mating was effective in changing the genetic arrangement of those populations by means of recombination of gene-linkage blocks. The F_2Syn5s tended to have greater G x E interactions than the F_2s, which was attributed to a reduction in the heterozygosity through the generations of random mating because some segregation occurred due to the breakup of some gene-linkage blocks. Some evidence suggests that the environmental variance is expected to be related to the level of heterozygosis (Robertson and Reeve 1952, Matzinger 1963).

The estimates of genetic variances among S_1 progenies of the F_2 and F_2Syn5 generations decreased significantly in B73xMo17 for dropped ears, ear diameter, cob diameter, row number, and days to silking, which suggest that coupling was the predominant linkage phase in these traits. The estimates of genetic variance in B73xB84, however, increased significantly for stalk lodging, ear length, ear index, prolificacy, kernel depth, and grain yield, suggesting that repulsion linkage phase was predominant for those traits in the cross of B73xB84. Therefore, objective one was partially fulfilled because there were some instances in both single crosses where the range of variability for some traits was increased. The estimates of genetic variance suggest that recombination was enhanced; those changes in the genetic variances reflected either changes in linkage disequilibrium or changes in allele frequency that occurred during the generations of random mating.

There was not always an increase in the phenotypic range of populations subjected to random mating, as was postulated by Baker (1968), or that repulsion phase linkages were not always predominant in the crosses of two unrelated inbred lines. The range of genetic variability, however, will not be increased in all instances (Hanson and Hayman, 1963; Baker, 1968), but the approach to the desired genotype could be achieved after some cycles of recurrent selection which includes recombination each cycle.

The estimates of heritability in both single crosses were higher for ear height, plant height, row number, and days to silking, which suggest that these traits were controlled by a relatively fewer number of genes and had lower G x E interaction. The heritability estimates for grain yield in B73xMo17 decreased from the F_2 to F_2Syn5 generations, attributed mainly to the higher G x E interaction in the F_2Syn5.

Significant changes in the genetic correlation coefficients were observed in 20.9% of the trait associations in B73xMo17; 68% of these changes increased from the F_2 to F_2Syn5, which suggest that the predominant linkage phase was repulsion. In B73xB84, there were 9.9% significant changes in the genetic correlations of trait associations, and, again, a higher proportion (60%) of the associations were observed to increase. The changes in correlations were similar to those reported by Miller and Rawlings (1967) and by Meredith and Bridge (1971) in cotton. In the B73xB84 cross, no change was observed between the associations of yield and all the traits measured. These results suggest that the objectives of random mating were partially fulfilled because recom-

bination between linkage-gene blocks was favored, almost twice the proportion in B73xMo17 as that in B73xB84.

Pleiotropism was excluded as the cause of the correlation between grain yield and three yield components (ear length, ear diameter, and kernel depth) because they had different predominant linkage phases. The genetic correlation between these traits did not increase, suggesting that these traits may be highly linked.

Insufficient evidence was obtained to support the use of random mating as a useful procedure prior to selfing in any breeding program. Some significant changes in means and variances were obtained, but in most instances the changes were relatively small. Sample sizes used in random mating and the number of generations of random mating seemed adequate, based on past theoretical and empirical studies. The number of S_1 progenies evaluated, however, may not have been adequate to adequately sample the range of extreme segregants obtained by recombination. Intuitively, it seems one or more generations of random mating would be advisable to the breakup of some trait associations. Random mating may not be as useful for crosses among related parents because the range of segregation is expected to be smaller, as was observed for B73xB84.

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APPENDIX A. ANALYSES OF VARIANCE AND PHENOTYPIC AND GENOTYPIC VARIANCES

Table A1. Analysis of variance, means, and coefficients of variation (C.V.) for five traits measured in three environments for the F_2 and random mated generations of four single crosses evaluated in 1984

Source of variation	df	Grain yield	Stand	Lodging		Dropped ears
				Root	Stalk	
		kg plot^{-1}	plants plot^{-1}	----------	%	----------
			Research Center			
Replications	2	12.1858**	18.375^{ns}	28.4008^{ns}	124.7481^{ns}	3.9657^{ns}
Entries	31	23.6738**	50.1021**	18.4053^{ns}	42.9547^{ns}	4.0617^{ns}
Error	62	1.4460	8.8159	14.7112	44.4945	3.9045
$\bar{X}$		12.1324	40.125	0.732	9.7719	0.862
C.V.		9.91	7.40	523.93	68.26	229.16
			Ankeny			
Replications	2	8.9345*	6.125^{ns}	16.9155*	71.718^{ns}	1.0712^{ns}
Entries	31	32.353**	16.0645*	3.8614^{ns}	74.1887*	3.1150**
Error	62	2.6115	9.4798	3.7969	40.2256	1.1268
$\bar{X}$		15.0362	47.00	1.030	10.3366	0.7855
C.V.		15.75	6.55	189.15	61.36	135.14
			Martinsburg			
Replications	2	4.1906^{ns}	1.2917^{ns}	348.7062^{ns}	0.3942^{ns}	12.8821*
Entries	31	18.200**	7.2903^{ns}	1109.7106*	58.5054**	3.5374^{ns}
Error	62	1.8863	4.5282	120.5239	27.8444	3.8420
$\bar{X}$		10.577	47.4167	22.8861	9.8094	1.4035
C.V.		12.98	4.49	47.97	53.79	139.66

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table A2. Analysis of variance, means, and coefficients of variation (C.V.) for five traits measured in three environments for the F_2 and random mated generations of four single crosses evaluated in 1985

Source of variation	df	Grain yield	Stand	Root	Stalk	Dropped ears
		kg plot^{-1}	plants plot^{-1}	----------	%----------	
			Research Center			
Replications	2	8.6266*	13.3229*	24.0851*	8.8847^{ns}	25.7613*
Entries	31	15.8391**	14.4503**	17.2665**	100.8337**	12.7088*
Error	62	2.1694	3.8928	5.1688	40.7935	6.4062
$\bar{X}$		11.5373	47.0208	1.7438	10.3592	3.1865
C.V.		12.77	4.20	130.37	61.65	79.43
			Ankeny			
Replications	2	18.4644**	76.3438*	54.8255**	103.2689^{ns}	9.0747^{ns}
Entries	31	20.9596**	23.4610^{ns}	12.5408*	447.2631**	5.4734^{ns}
Error	62	2.2171	16.0104	6.5871	111.8593	4.8284
$\bar{X}$		7.239	41.6875	1.6435	27.8439	1.58
C.V.		20.57	9.5983	156.17	37.99	139.0
			Martinsburg			
Replications	2	5.2684^{ns}	6.0142^{ns}	24.6158^{ns}	9.39^{ns}	2.0964^{ns}
Entries	31	17.3790**	17.6452^{ns}	73.5387**	20.6792^{ns}	2.7618^{ns}
Error	62	2.0331	12.2792	34.1073	17.1074	2.6789
$\bar{X}$		11.10	45.9583	5.2682	5.4713	0.9478
C.V.		12.85	7.62	110.86	75.60	172.69

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table A3. Analysis of variance, means, and coefficients of variation (C.V.) for 13 traits measured in 100 S_1 progenies of F_2 and F_2 Syn 5 generations of two single crosses in experiments conducted at the Research Center in 1984

Source of variation	df	Mean squares		
		Lodging		Dropped ears
		Root	Stalk	
		----------%		
Sets	9	2.53^{ns}	198.62**	15.15**
Rep (Sets)	10	1.38^{ns}	111.17*	10.11**
Entries (Sets)	390	2.57*	90.38**	8.97**
(B73 x Mo17)F_2	90	1.06^{ns}	144.43**	14.34**
(B73 x Mo17)F_2 Syn 5	90	2.52^{ns}	88.29**	11.96
(B73 x B84)F_2	90	2.76^{ns}	53.65^{ns}	4.06^{ns}
(B73 x B84)F_2 Syn 5	90	3.94**	57.12^{ns}	2.14^{ns}
(B73 x Mo17)F_2 Syn 5	10	2.39^{ns}	156.40**	11.83*
(B73 x B84)F_2 vs F_2 Syn 5	10	2.84^{ns}	54.02^{ns}	2.68^{ns}
(B73 x Mo17) vs (B73 x B84)	10	2.39^{ns}	223.00**	42.73**
Error	390	2.16	51.18	4.89
Total	799			
Mean		0.3265	6.8512	1.00
C.V.		450.35	104.42	221.22

[a]Expressed as the ratio of ear height to plant height.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

Mean squares						
Height		Ear	Diameter			
Plant	Ear	length	Ear	Cob	Ear index[a]	Prolificacy
---cm---						no.
400.31**	373.46**	7.80**	0.499**	0.241**	0.0064**	0.0359*
33.83[ns]	96.65**	3.90**	0.039[ns]	0.021[ns]	0.0015**	0.0200[ns]
486.87**	209.85**	4.08**	0.067**	0.050**	0.0021**	0.030**
472.30**	231.00**	2.68**	0.094**	0.044**	0.0016**	0.0307**
462.18**	275.33**	2.45**	0.076**	0.022**	0.0025**	0.0326**
274.95**	124.77**	1.97**	0.044**	0.030**	0.0014**	0.0115**
219.62**	129.14**	2.44**	0.050**	0.033**	0.0016**	0.0316**
746.70**	543.59**	2.64**	0.114**	0.046**	0.0036**	0.0057[ns]
1797.29**	622.89**	3.36**	0.055**	0.013[ns]	0.0013**	0.0226[ns]
3582.68**	168.28**	67.02**	0.060**	0.723**	0.0126**	0.1648**
86.43	39.29	0.85	0.022	0.014	0.0004	0.0148
188.42	90.99	14.99	4.39	2.79	0.482	0.99
4.93	6.89	6.14	3.35	4.21	4.31	12.27

Table A3. (Continued)

Source of variation	df	Mean squares: Kernel depth	Row number	Yield
		cm	no.	kg ha^{-1}
Sets	9	0.0179**	4.732**	2586.61**
Rep (Sets)	10	0.0067^{ns}	0.475^{ns}	951.14*
Entries (Sets)	390	0.0157**	5.49**	1367.15**
(B73 x Mo17)F_2	90	0.0106**	4.07**	1732.23**
(B73 x Mo17)F_2 Syn 5	90	0.0135**	2.23**	1591.65**
(B73 x B84)F_2	90	0.0096*	4.02**	889.09**
(B73 x B84)F_2 Syn 5	90	0.0092*	3.85**	947.84**
(B73 x Mo17)F_2 vs F_2 Syn 5	10	0.0199**	2.91**	1620.59*
(B73 x B84)F_2 vs F_2 Syn 5	10	0.0125*	5.01**	540.33^{ns}
(B73 x Mo17) vs (B73 x B84)	10	0.1934**	78.62**	4710.56**
Error	390	0.0062	0.54	443.92
Total	799			
Mean		0.7979	16.42	4331.77
C.V.		9.90	4.47	15.38

Table A4. Analysis of variance, means, and coefficients of variation (C.V.) for 13 traits measured in 100 S_1 progenies of F_2 and F_2 Syn 5 generations of two single crosses in experiments conducted at the Atomic Energy Center in 1984

Source of variation	df	Mean squares		
		Lodging		Dropped ears
		Root	Stalk	
		----------%----------		
Sets	9	0.428^{ns}	43.95**	1.92^{ns}
Rep (Sets)	10	0.970^{ns}	12.43^{ns}	1.16^{ns}
Entries (Sets)	390	0.84^{ns}	16.88**	1.60^{ns}
(B73 x Mo17)F_2	90	1.26*	19.94**	0.50^{ns}
(B73 x Mo17)F_2 Syn 5	90	1.86**	12.69^{ns}	2.92**
(B73 x B84)F_2	90	0.11^{ns}	15.23*	0.64^{ns}
(B73 x B84)F_2 Syn 5	90	0.11^{ns}	18.62**	2.13^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	10	1.59**	23.79**	2.47^{ns}
(B73 x B84)F_2 vs F_2 Syn 5	10	0.11^{ns}	10.14^{ns}	1.72^{ns}
(B73 x Mo17) vs (B73 x B84)	10	1.00^{ns}	26.07**	2.38^{ns}
Error	390	0.85	10.86	1.67
Total	799			
Mean		0.1159	1.93	0.16
C.V.		796.85	170.43	788.31

[a]Expressed as the ratio of ear height to plant height.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

Mean squares						
Height		Ear	Diameter			
Plant	Ear	length	Ear	Cob	Ear index[a]	Prolificacy
cm						no.
389.52**	369.47**	2.19**	0.147**	0.083**	0.0034**	0.166**
241.62*	119.57*	1.22^{ns}	0.082**	0.014^{ns}	0.0006^{ns}	0.033*
477.29**	253.71**	4.52**	0.063**	0.048**	0.0025**	0.051**
448.68**	296.47**	3.30**	0.088**	0.042**	0.0021**	0.034**
455.75**	306.30**	3.07**	0.072**	0.038**	0.0026**	0.052**
262.97**	161.39**	1.83**	0.043**	0.032**	0.0015**	0.044**
269.45**	170.97**	2.02**	0.045**	0.030**	0.0019**	0.032**
1008.43**	737.10**	4.65**	0.095**	0.039**	0.0035**	0.069**
1395.57**	528.07**	2.51**	0.066**	0.017^{ns}	0.0017**	0.037**
3278.86**	213.43**	77.04**	0.068**	0.523**	0.0178**	0.447**
77.28	54.70	0.92	0.026	0.015	0.0006	0.015
200.83	100.24	14.80	4.28	2.71	0.4985	0.993
4.38	7.38	16.48	3.75	4.52	5.05	12.53

Table A4. (Continued)

Source of variation	df	Mean squares: Kernel depth	Row number	Yield
		cm	no.	kg ha^{-1}
Sets	9	0.034**	4.55**	1891.53**
Rep (Sets)	10	0.015**	0.49^{ns}	3466.12**
Entries (Sets)	390	0.015**	4.71**	1175.94**
(B73 x Mo17)F_2	90	0.015**	3.48**	1682.31**
(B73 x Mo17)F_2 Syn 5	90	0.011**	2.23**	1495.01**
(B73 x B84)F_2	90	0.010**	3.52**	720.03**
(B73 x B84)F_2 Syn 5	90	0.008^{ns}	3.17**	688.34**
(B73 x Mo17)F_2 vs F_2 Syn 5	10	0.014*	3.51**	1385.33**
(B73 x B84)F_2 vs F_2 Syn 5	10	0.012*	4.74**	445.90^{ns}
(B73 x Mo17) vs (B73 x B84)	10	0.168**	63.91**	2759.12**
Error	390	0.006	0.614	432.76
Total	799			
Mean		0.7889	16.18	4143.01
C.V.		9.51	4.84	15.88

Table A5. Analysis of variance, means, and coefficients of variation (C.V.) for 14 traits measured in 100 S_1 progenies of F_2 and F_2 Syn 5 generations of two single crosses in experiments conducted at the Research Center in 1985

Source of variation	df	Mean squares		
		Lodging		Dropped ears
		Root	Stalk	
		----------%----------		
Sets	9	299.42**	1444.79**	1.94^{ns}
Rep (Sets)	10	70.73^{ns}	94.22^{ns}	2.04^{ns}
Entries (Sets)	390	193.10**	304.70**	5.19**
(B73 x Mo17)F_2	90	119.25**	345.70**	9.65**
(B73 x Mo17)F_2 Syn 5	90	52.26^{ns}	420.78**	7.49**
(B73 x B84)F_2	90	272.73**	134.02**	1.57^{ns}
(B73 x B84)F_2 Syn 5	90	255.28**	242.31**	1.15^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	10	89.86^{ns}	175.33**	3.90^{ns}
(B73 x B84)F_2 vs F_2 Syn 5	10	216.33**	273.54**	0.76^{ns}
(B73 x Mo17) vs (B73 x B84)	10	929.09**	1149.07**	19.02**
Error	390	63.19	69.24	3.21
Total	799			
Mean		6.27	11.10	0.71
C.V.		126.74	74.96	250.92

[a]Expressed at the ratio of ear height to plant height.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

Mean squares						
Height		Ear	Diameter			
Plant	Ear	length	Ear	Cob	Ear index[a]	Prolificacy
						no.
4700.41**	847.41**	4.56**	0.106**	0.044**	0.0208**	0.054**
222.44**	51.80[ns]	1.46[ns]	0.031*	0.017[ns]	0.0006[ns]	0.014[ns]
422.14**	240.50**	5.50**	0.072**	0.052**	0.0025**	0.039**
458.26**	251.29**	3.17**	0.089**	0.044**	0.0019**	0.019**
445.69**	310.35**	2.96**	0.072**	0.025**	0.0032**	0.059**
263.92**	137.59**	2.72**	0.039**	0.038**	0.0015**	0.025**
317.74**	156.49**	3.30**	0.050**	0.032**	0.0017	0.029**
1018.25**	894.26**	8.32**	0.052**	0.042**	0.0007[ns]	0.083**
1165.72**	402.01**	2.08**	0.052**	0.031*	0.0002[ns]	0.028**
909.03**	382.03**	94.70**	0.443**	0.711**	0.0016**	0.217**
64.25	28.93	0.79	0.015	0.015	0.0004	0.010
186.26	91.10	15.68	4.49	2.66	0.089	0.99
4.30	5.90	5.68	2.73	4.56	4.20	10.27

Table A5. (Continued)

Source of variation	df	Mean squares			
		Kernel depth	Row number	Yield	Days to silking
		cn	no.	kg ha^{-1}	no.
Sets	9	0.016*	2.54**	3888.22**	24.51**
Rep (Sets)	10	0.014*	0.55^{ns}	1274.17**	6.74**
Entries (Sets)	390	0.014**	4.44**	2238.95**	11.80
(B73 x Mo17)F_2	90	0.014**	3.04**	2416.96**	13.90**
(B73 x Mo17)F_2 Syn 5	90	0.015**	2.40**	2946.82**	10.66**
(B73 x B84)F_2	90	0.011**	3.45**	1365.41**	4.15**
(B73 x B84)F_2 Syn 5	90	0.013**	3.07**	1842.53**	6.97**
(B73 x Mo17)F_2 vs F_2 Syn 5	10	0.009^{ns}	3.17**	5736/21**	31.90**
(B73 x B84)F_2 F_2 Syn 5	10	0.015*	4.29	1271.74**	2.77^{ns}
(B73 x Mc17) vs (B73 x B84)	10	0.039**	57.97**	3165.66**	104.25**
Error	390	0.007	0.628	486.92	1.56
Total	799				
Mean		0.92	15.65	5932.72	84.62
C.V.		9.00	5.06	11.76	1.48

Table A6. Analysis of variance, means, and coefficients of variation (C.V.) for 14 traits measured in 100 S_1 progenies of F_2 and F_2 Syn 5 generations of two single crosses in experiments conducted at the Research Center in 1985

Source of variation	df	Mean squares		
		Lodging		Dropped ears
		Root	Stalk	
		----------%----------		
Sets	9	1307.72**	71.26^{ns}	0.155^{ns}
Rep (Sets)	10	110.49^{ns}	131.86**	0.363^{ns}
Entries (Sets)	390	229.93**	142.17**	0.308^{ns}
(B73 x Mo17)F_2	90	118.09^{ns}	164.86**	0.227^{ns}
(B73 x Mo17)F_2 Syn 5	90	137.13^{ns}	262.97**	0.454*
(B73 x B84)F_2	90	323.70**	48.38^{ns}	0.342^{ns}
(B73 x B84)F_2 Syn 5	90	269.54**	72.24*	0.227^{ns}
(B73 x Mo17)F_2 vs F_2 Syn 5	10	135.28^{ns}	151.44**	0.227^{ns}
(B73 x B84)F_2 vs F_2 Syn 5	10	158.17^{ns}	93.45*	0.165^{ns}
(B73 x Mo17) vs (B73 x B84)	10	1037.77**	363.91**	0.374^{ns}
Error	390	106.38	47.53	0.311
Total	799			
Mean		7.28	5.75	851.18
C.V.		141.75	119.94	0.065

[a]Expressed at the ratio of ear height to plant height.

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

Mean squares						
Height		Ear	Diameter			
Plant	Ear	lenght	Ear	Cob	Ear index[a]	Prolificacy
---cm---						no.
730.84**	184.49**	9.47**	0.074**	0.022^{ns}	0.0023**	0.022**
104.63**	101.65**	1.95*	0.018^{ns}	0.011^{ns}	0.0014*	0.006^{ns}
351.38**	184.23**	4.50**	0.083**	0.050**	0.0028**	0.042**
299.30**	182.66**	3.43**	0.115**	0.046**	0.0019**	0.026**
279.65**	204.61**	3.01**	0.084**	0.035**	0.0029**	0.047**
194.54**	133.25**	2.36**	0.051**	0.025**	0.0019**	0.015**
210.31**	143.75**	3.54**	0.070**	0.025**	0.0023**	0.030**
985.23**	587.26**	8.18**	0.048*	0.022^{ns}	0.0029**	0.079**
1066.92**	432.95**	1.15^{ns}	0.091**	0.019^{ns}	0.0001^{ns}	0.017*
2797.41**	186.14**	55.15**	0.207**	0.718**	0.0024**	0.458**
39.38	28.19	0.99	0.025	0.014	0.0006	0.008
164.24	88.02	14.14	4.36	2.70	0.536	0.94
3.82	6.03	7.02	3.62	4.34	4.65	9.47

Table A6. (Continued)

Source of variation	df	Mean squares: Kernel depth	Row number	Yield	Days to silking
		cm		kg ha^{-1}	
Sets	9	0.021**	5.97**	1040.42**	29.03**
Rep (Sets)	10	0.010^{ns}	0.28^{ns}	178.77^{ns}	2.82^{ns}
Entries (Sets)	390	0.017**	4.01**	1859.76**	12.50**
(B73 x Mo17)F_2	90	0.017**	3.16**	1921.52**	13.19**
(B73 x Mo17)F_2 Syn 5	90	0.015**	2.43**	2299.30**	10.03**
(B73 x B84)F_2	90	0.011^{ns}	3.20**	1378.08**	9.08**
(B73 x B84)F_2 Syn 5	90	0.017**	2.65**	1792.19**	8.61**
(B73 x Mo17)F_2 vs F_2 Syn 5	10	0.011^{ns}	3.23**	4070.36**	18.55**
(B73 x B84)F_2 vs F_2 Syn 5	10	0.015^{ns}	3.88**	1153.78*	4.51*
(B73 x Mo17) vs (B73 x B84)	10	0.102**	46.30**	785.71^{ns}	96.22**
Error	390	0.008	0.72	397.71	1.97
Total	799				
Mean		0.829	15.53	4348.46	86.13
C.V.		11.09	5.48	14.50	1.63

Table A7. Mean values ($\bar{X}$) and coefficients of variation (C.V.) for 13 traits measured in 100 S_1 lines derived in the F_2 and F_2 Syn 5 generations from two single crosses (Research Center, 1984)

	B73 x Mo17				B73 x B84			
	F_2		F_2 Syn 5		F_2		F_2 Syn 5	
Traits	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.
Root lodging, %	0.24	455.0	0.32	370.4	0.39	460.2	0.35	479.2
Stalk lodging, %	8.98	95.4	6.52	110.0	5.81	106.8	6.10	107.6
Dropped ears, %	1.55	169.2	1.63	175.6	0.49	267.5	0.33	469.0
Plant height, cm	198.6	4.87	191.03	4.17	188.29	4.79	175.79	5.55
Ear height, cm	95.0	7.44	88.8	6.58	93.7	6.58	86.4	6.60
Ear length, cm	16.03	6.17	15.75	5.93	13.95	6.73	14.25	5.53
Ear diameter, cm	4.37	3.25	4.40	3.74	4.36	3.20	4.41	3.08
Cob diameter, cm	2.71	3.79	2.68	3.94	2.88	4.03	2.89	4.55
Ear index[a]	0.477	4.51	0.464	4.70	0.498	4.22	0.491	3.88
Prolificacy, no.	0.95	11.16	0.95	15.90	1.04	8.86	1.03	12.73
Kernel depth, cm	0.83	8.80	0.86	10.38	0.74	10.94	0.76	9.73
Row number, no.	15.32	4.18	15.55	4.72	17.18	4.36	17.61	4.29
Yield, kg ha^{-1}	4617.8	13.91	4430.4	14.78	4160.5	15.88	4118.3	15.9

[a]Expressed as the ratio of ear height to plant height.

Table A8. Mean values ($\bar{X}$) and coefficients of variation (C.V.) for 13 traits measured in 100 S_1 lines derived in the F_2 and F_2 Syn 5 generations from two single crosses (Atomic Energy Center, 1984)

	B73 x Mo17				B73 x B84			
	F_2		F_2 Syn 5		F_2		F_2 Syn 5	
Traits	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.
Root lodging, %	0.17	668.4	0.25	548.9	0.02	1414.2	0.02	1414.2
Stalk lodging, %	2.30	144.3	1.34	185.8	2.05	172.1	2.05	164.8
Dropped ears, %	0.12	647.6	0.29	609.2	0.09	859.5	0.15	1030.0
Plant height, cm	211.3	4.32	202.5	4.61	200.2	4.43	189.4	4.03
Ear height, cm	104.3	7.44	96.8	8.28	102.9	6.96	97.0	6.84
Ear length, cm	16.02	6.11	15.52	7.29	13.69	5.90	13.99	6.36
Ear diameter, cm	4.30	3.50	4.29	4.37	4.25	3.28	4.30	3.60
Cob diameter, cm	2.65	4.44	2.61	5.65	2.77	3.98	2.88	3.99
Ear index[a]	2.493	5.09	0.477	5.48	0.513	4.88	0.512	4.89
Prolificacy, no.	0.94	12.37	0.90	13.21	1.08	12.76	1.04	11.86
Kernel depth, no.	0.83	8.97	0.84	9.31	0.74	9.92	0.75	10.44
Row number, no.	15.21	4.64	15.37	5.25	16.82	4.62	17.30	4.61
Yield, kg ha^{-1}	4373.5	16.33	4158.5	17.26	4064.5	14.39	3975.6	15.14

[a]Expressed as the ratio of ear height to plant height.

Table A9. Mean values ($\bar{X}$) and coefficients of variation (C.V.) for 14 traits measured in 100 S_1 lines derived in the F_2 and F_2 Syn 5 generations from two single crosses (Research Center, 1985)

	B73 x Mo17				B73 x B84			
	F_2		F_2 Syn 5		F_2		F_2 Syn 5	
Traits	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.
Root lodging, %	4.06	134.4	2.74	191.6	9.20	110.2	9.08	106.8
Stalk lodging, %	13.73	68.51	12.97	72.31	8.04	80.74	9.67	78.54
Dropped ears, %	1.11	181.2	1.18	208.1	0.32	375.8	0.25	448.1
Plant height, cm	192.8	3.70	183.8	4.01	189.3	4.78	179.1	4.62
Ear height, cm	94.0	5.70	85.4	6.01	95.5	6.06	89.6	5.87
Ear length, cm	17.04	5.48	16.48	5.87	14.51	6.16	14.70	5.16
Ear diameter, cm	4.41	2.84	4.44	2.62	4.52	2.91	4.58	2.69
Cob diameter, cm	2.57	4.65	2.55	4.50	2.74	4.39	2.75	4.38
Ear index[a]	0.487	3.88	0.463	4.60	0.504	4.48	0.500	3.88
Prolificacy, no.	0.95	10.27	0.93	11.09	1.04	9.23	1.04	9.93
Kernel depth, cm	0.92	9.24	0.94	7.40	0.89	9.41	0.91	9.86
Row number, no.	14.66	5.25	14.97	5.29	16.24	5.01	16.73	4.86
Yield, kg ha^{-1}	6250.1	10.47	5784.8	15.42	5881.3	10.73	5814.7	9.23
Days to silking, %	84.12	1.24	82.90	1.78	84.9	1.54	85.57	1.37

[a]Expressed as the ratio of ear height to plant height.

Table A10. Mean values ($\bar{X}$) and coefficients of variation (C.V.) for 14 traits measured in 100 S_1 lines derived in the F_2 and F_2 Syn 5 generations from two single crosses (Atomic Energy Research Center, 1985)[2]

	B73 x Mo17				B73 x B84			
	F_2		F_2 Syn 5		F_2		F_2 Syn 5	
Traits	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.	$\bar{X}$	C.V.
Root lodging, %	5.32	151.7	3.75	160.2	10.15	115.7	9.88	139.8
Stalk lodging, %	7.22	80.44	7.19	85.94	3.84	155.8	4.73	185.6
Dropped ears, %	0.55	1000.0	0.10	707.1	0.07	817.1	0.05	1000.0
Plant height, cm	174.4	3.87	165.5	3.13	163.5	4.51	153.6	3.75
Ear height, cm	91.7	6.64	85.2	5.85	90.6	5.95	84.6	5.48
Ear length, cm	15.28	7.82	14.62	6.25	13.29	5.92	13.39	7.77
Ear diameter, cm	4.32	3.86	4.34	3.65	4.35	3.80	4.42	3.40
Cob diameter, cm	2.61	4.90	2.60	4.07	2.78	3.92	2.80	4.00
Ear index[a]	0.525	4.84	0.514	4.62	0.554	4.65	0.550	4.38
Prolificacy, no.	0.89	10.21	0.84	10.12	1.03	7.78	1.00	9.82
Kernel depth, cm	0.85	12.22	0.87	9.55	0.78	12.50	0.81	10.42
Row number, no.	14.62	5.15	14.96	5.78	16.07	5.69	16.46	5.30
Yield, kg ha^{-1}	4515.0	18.00	4177.0	13.82	4389.0	11.82	4312.9	13.35
Days to silking, no.	85.56	1.73	84.59	1.63	87.33	1.42	87.03	1.74

[a]Expressed as the ratio of ear height to plant height.

Table A11. Observed changes in the mean of the F_2 relative to the F_2 Syn 5 of two single crosses expressed as percent of the F_2 mean (Research Center and Atomic Energy Center, 1984 and 1985)

	1984				1985			
	Exp 21		Exp 22		Exp 23		Exp 24	
Traits	A[a]	B[a]	A	B	A	B	A	B
Root lodging, %	130.74	88.58	147.62	100.0	67.49	98.70	70.49	97.34
Stalk lodging, %	72.61	104.99	58.26	100.0	94.46	120.27	99.58	123.18
Dropped ears, %	105.16	67.35	241.67	166.67	106.31	78.13	197.92	66.67
Plant height, cm	96.19	93.36	95.85	94.60	95.35	94.62	94.90	93.95
Ear height, cm	93.47	92.21	92.81	94.27	90.84	93.83	92.91	93.36
Ear length, cm	98.25	102.15	96.88	102.19	96.71	101.31	95.68	100.75
Ear diameter, cm	100.69	101.15	99.77	101.18	100.68	101.33	100.46	101.61
Cob diameter, cm	98.80	100.35	98.49	101.08	99.22	100.36	99.62	100.72
Ear index[b]	97.27	98.59	96.75	99.81	95.07	99.21	97.90	99.28
Prolificacy, no.	100.0	99.04	95.74	96.30	97.89	100.0	94.38	97.09
Kernel depth, cm	103.61	102.7	101.20	101.35	102.17	102.25	102.35	103.85
Row number, no.	101.50	102.5	101.05	102.85	102.11	103.02	102.33	102.43
Yield, kg ha^{-1}	95.94	98.99	95.08	97.81	92.56	98.87	92.52	98.27

[a]A indicates B73 x Mo17 and B indicates B73 x B84.

[b]Expressed as the ratio of ear height to plant height.

Table A12. Genetic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Research Center, 1984

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	-0.552 ± 0.11	0.181 ± 0.20
Stalk lodging, %	46.62 ± 10.80	18.55 ± 6.76
Dropped ears, %	4.73 ± 1.07	3.54 ± 0.90
Plant height, cm	192.93 ± 34.95	187.87 ± 34.21
Ear height, cm	95.85 ± 17.09	118.02 ± 20.35
Ear length, cm	0.918 ± 0.20	0.80 ± 0.18
Ear diameter, cm	0.036 ± 0.01	0.027 ± 0.006
Cob diameter, cm	0.015 ± 0.003	0.004 ± 0.002
Ear index[a]	0.00061 ± 0.00012	0.00106 ± 0.00019
Prolificacy, no.	0.008 ± 0.002	0.009 ± 0.003
Kernel depth, cm	0.002 ± 0.001	0.004 ± 0.001
Row number, no.	1.77 ± 0.3	0.84 ± 0.17
Grain yield, kg ha^{-1}	644.2 ± 128.7	573.9 ± 118.4

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
0.298 ± 0.22	0.890 ± 0.30
1.23 ± 4.36	2.97 ± 4.59
-0.412 ± 0.35	-1.38 ± 0.24
94.26 ± 20.50	66.59 ± 16.48
43.13 ± 9.36	44.92 ± 9.62
0.563 ± 0.15	0.797 ± 0.18
0.011 ± 0.003	0.014 ± 0.004
0.008 ± 0.002	0.010 ± 0.003
0.00047 ± 0.001	0.00058 ± 0.00012
-0.002 ± 0.001	0.008 ± 0.002
0.002 ± 0.001	0.002 ± 0.001
1.74 ± 0.30	1.66 ± 0.28
222.6 ± 67.4	251.9 ± 71.7

Table A13. Genetic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Atomic Energy Center, 1984

Traits	Single crosses			
	B73 x Mo17		B73 x B84	
	F_2	F_2 Syn 5	F_2	F_2 Syn 5
Root lodging, %	0.203 ± 0.098	0.516 ± 0.14	-0.37 ± 0.03	-0.37 ± 0.03
Stalk lodging, %	4.54 ± 1.5	0.91 ± 1.01	2.19 ± 1.19	3.88 ± 1.43
Dropped ears, %	-0.58 ± 0.07	0.63 ± 0.22	-0.51 ± 0.08	0.23 ± 0.17
Plant height, cm	185.7 ± 33.2	189.2 ± 33.7	92.8 ± 19.6	96.1 ± 20.1
Ear height, cm	120.9 ± 21.9	125.8 ± 22.7	53.3 ± 12.1	58.1 ± 12.7
Ear length, cm	1.19 ± 0.25	1.08 ± 0.23	0.45 ± 0.14	0.55 ± 0.15
Ear diameter, cm	0.031 ± 0.007	0.023 ± 0.005	0.009 ± 0.003	0.1 ± 0.004
Cob diameter, cm	0.014 ± 0.003	0.012 ± 0.003	0.009 ± 0.002	0.007 ± 0.002
Ear index[a]	0.00074 ± 0.0002	0.001 ± 0.0002	0.00043 ± 0.0001	0.00066 ± 0.00014
Prolificacy, no.	0.009 ± 0.003	0.018 ± 0.004	0.015 ± 0.003	0.008 ± 0.002
Kernel depth, cm	0.005 ± 0.001	0.003 ± 0.001	0.002 ± 0.001	0.0014 ± 0.0007
Row number, no.	1.43 ± 0.26	0.81 ± 0.17	1.45 ± 0.26	1.28 ± 0.23
Grain yield, kg ha^{-1}	624.8 ± 125.0	531.1 ± 111.3	143.6 ± 55.3	127.8 ± 53.0

[a]Expressed as the ratio of ear height to plant height.

Table A14. Genetic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Research Center, 1985

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	28.03 ± 9.1	-5.47 ± 4.5
Stalk lodging, %	138.2 ± 25.6	175.8 ± 31.1
Dropped ears, %	3.22 ± 0.72	2.14 ± 0.56
Plant height, cm	197.0 ± 33.9	190.7 ± 32.9
Ear height, cm	111.2 ± 18.6	140.7 ± 22.9
Ear length, cm	1.19 ± 0.24	1.08 ± 0.22
Ear diameter, cm	0.037 ± 0.007	0.029 ± 0.005
Cob diameter, cm	0.015 ± 0.003	0.005 ± 0.002
Ear index[a]	0.00075 ± 0.00014	0.0014 ± 0.0002
Prolificacy, no.	0.005 ± 0.002	0.025 ± 0.004
Kernel depth, cm	0.004 ± 0.001	0.004 ± 0.001
Row number, no.	1.21 ± 0.23	0.89 ± 0.18
Grain yield, kg ha^{-1}	965.0 ± 179.0	1230.0 ± 217.9
Days to silking, %	6.17 ± 1.03	4.55 ± 0.79

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
104.8 ± 20.2	96.0 ± 18.9
32.4 ± 10.2	86.5 ± 18.0
-0.82 ± 0.16	-1.03 ± 0.14
99.8 ± 19.6	111.7 ± 21.3
54.3 ± 10.2	63.8 ± 11.6
0.96 ± 0.20	1.25 ± 0.24
0.012 ± 0.003	0.017 ± 0.004
0.012 ± 0.003	0.009 ± 0.003
0.0005 ± 0.0001	0.0006 ± 0.0001
0.007 ± 0.002	0.010 ± 0.002
0.002 ± 0.001	0.003 ± 0.001
1.41 ± 0.26	1.22 ± 0.23
439.2 ± 102.2	677.8 ± 136.9
1.30 ± 0.31	2.71 ± 0.52

Table A15. Genetic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Atomic Energy Center, 1985

Traits	Single crosses B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	5.85 ± 9.5	15.4 ± 10.8
Stalk lodging, %	58.7 ± 12.3	107.7 ± 19.5
Dropped ears, %	-0.04 ± 0.02	0.071 ± 0.035
Plant height, cm	130.0 ± 22.1	120.1 ± 20.7
Ear height, cm	77.2 ± 13.5	88.2 ± 15.1
Ear length, cm	1.22 ± 0.26	1.01 ± 0.22
Ear diameter, cm	0.045 ± 0.009	0.03 ± 0.006
Cob diameter, cm	0.016 ± 0.003	0.011 ± 0.003
Ear index[a]	0.00064 ± 0.00014	0.0012 ± 0.0002
Prolificacy, no.	0.009 ± 0.002	0.020 ± 0.004
Kernel depth, cm	0.004 ± 0.0013	0.0032 ± 0.0011
Row number, no.	1.22 ± 0.23	0.85 ± 0.18
Grain yield, kg ha^{-1}	761.9 ± 142.4	950.8 ± 170.1
Days to silking, %	5.61 ± 0.97	4.03 ± 0.74

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
108.7 ± 24.2	81.6 ± 20.2
0.43 ± 3.9	12.4 ± 5.6
0.015 ± 0.028	-0.042 ± 0.02
77.6 ± 14.4	85.5 ± 15.6
52.5 ± 9.9	57.8 ± 10.6
0.69 ± 0.18	1.28 ± 0.26
0.013 ± 0.004	0.023 ± 0.005
0.006 ± 0.002	0.006 ± 0.002
0.00063 ± 0.00014	0.0008 ± 0.0002
0.004 ± 0.001	0.011 ± 0.002
0.0012 ± 0.0009	0.0041 ± 0.0013
1.24 ± 0.24	0.96 ± 0.20
490.2 ± 102.6	697.2 ± 132.9
3.56 ± 0.67	3.32 ± 0.64

Table A16. Phenotypic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Research Center, 1984

Traits	Single crosses			
	B73 x Mo17		B73 x B84	
	F_2	F_2 Syn 5	F_2	F_2 Syn 5
Root lodging, %	0.53 ± 0.08	1.26 ± 0.19	1.38 ± 0.20	1.97 ± 0.29
Stalk lodging, %	72.2 ± 10.6	44.1 ± 6.5	26.8 ± 3.9	28.6 ± 4.2
Dropped ears, %	7.17 ± 1.1	5.98 ± 0.9	2.03 ± 0.3	1.07 ± 0.16
Plant height, cm	236.1 ± 34.8	231.1 ± 34.1	137.5 ± 20.3	109.8 ± 16.2
Ear height, cm	115.5 ± 17.0	137.7 ± 20.3	62.8 ± 9.3	64.6 ± 9.5
Ear length, cm	1.34 ± 0.2	1.22 ± 0.2	0.99 ± 0.15	1.22 ± 0.18
Ear diameter, cm	0.047 ± 0.007	0.038 ± 0.006	0.022 ± 0.003	0.025 ± 0.004
Cob diameter, cm	0.022 ± 0.003	0.011 ± 0.002	0.015 ± 0.002	0.017 ± 0.003
Ear index[a]	0.00082 ± 0.00012	0.0013 ± 0.0002	0.0007 ± 0.0001	0.0008 ± 0.0001
Prolificacy, no.	0.015 ± 0.002	0.016 ± 0.002	0.006 ± 0.0009	0.016 ± 0.002
Kernel depth, cm	0.005 ± 0.001	0.007 ± 0.001	0.005 ± 0.001	0.005 ± 0.001
Row number, no.	2.04 ± 0.30	1.11 ± 0.16	2.01 ± 0.30	1.93 ± 0.28
Grain yield, kg ha^{-1}	866.1 ± 127.7	795.8 ± 117.3	444.5 ± 65.5	473.9 ± 69.9

[a]Expressed as the ratio of ear height to plant height.

Table A17. Phenotypic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations from two single crosses evaluated at the Atomic Energy Center, 1984

Traits	Single crosses			
	B73 x Mo17		B73 x B84	
	F_2	F_2 Syn 5	F_2	F_2 Syn 5
Root lodging, %	0.63 ± 0.09	0.94 ± 0.14	0.057 ± 0.008	0.057 ± 0.008
Stalk lodging, %	9.97 ± 1.47	6.34 ± 0.94	7.62 ± 1.12	9.31 ± 1.37
Dropped ears, %	0.25 ± 0.04	1.46 ± 0.22	0.32 ± 0.05	1.06 ± 0.16
Plant height, cm	224.3 ± 33.1	227.9 ± 33.6	131.5 ± 19.5	134.7 ± 19.9
Ear height, cm	148.2 ± 21.9	153.1 ± 22.6	80.7 ± 11.9	85.5 ± 12.6
Ear length, cm	1.65 ± 0.24	1.54 ± 0.23	0.91 ± 0.13	1.01 ± 0.15
Ear diameter, cm	0.044 ± 0.007	0.036 ± 0.005	0.022 ± 0.003	0.023 ± 0.003
Cob diameter, cm	0.021 ± 0.003	0.019 ± 0.003	0.016 ± 0.002	0.015 ± 0.002
Ear index[a]	0.0011 ± 0.0022	0.0013 ± 0.0002	0.0007 ± 0.0001	0.0010 ± 0.0001
Prolificacy, no.	0.017 ± 0.003	0.026 ± 0.004	0.022 ± 0.003	0.016 ± 0.002
Kernel depth, cm	0.007 ± 0.001	0.006 ± 0.001	0.005 ± 0.001	0.004 ± 0.001
Row number, no.	1.74 ± 0.26	1.11 ± 0.16	1.76 ± 0.26	1.58 ± 0.023
Grain yield, kg ha^{-1}	841.2 ± 124.0	747.5 ± 110.2	360.0 ± 53.1	344.2 ± 50.7

[a]Expressed as the ratio of ear height to plant height.

Table A18. Phenotypic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Research Center, 1985

Traits	Single crosses			
	B73 x Mo17		B73 x B84	
	F_2	F_2 Syn 5	F_2	F_2 Syn 5
Root lodging, %	59.6 ± 8.8	26.1 ± 3.9	136.4 ± 20.1	127.6 ± 18.8
Stalk lodging, %	172.9 ± 25.5	210.4 ± 31.0	67.0 ± 9.9	121.2 ± 17.9
Dropped ears, %	4.83 ± 0.71	3.74 ± 0.55	0.79 ± 0.12	0.57 ± 0.08
Plant height, cm	229.1 ± 33.8	222.8 ± 32.9	132.0 ± 19.5	143.9 ± 21.2
Ear height, cm	125.6 ± 18.5	155.2 ± 22.9	68.8 ± 10.1	78.2 ± 11.5
Ear length, cm	1.59 ± 0.23	1.48 ± 0.22	1.36 ± 0.20	1.65 ± 0.24
Ear diameter, cm	0.045 ± 0.007	0.036 ± 0.005	0.020 ± 0.003	0.025 ± 0.004
Cob diameter, cm	0.022 ± 0.003	0.013 ± 0.002	0.019 ± 0.003	0.016 ± 0.002
Ear index[a]	0.0010 ± 0.0001	0.0016 ± 0.0002	0.0007 ± 0.0001	0.0008 ± 0.0001
Prolificacy, no.	0.010 ± 0.001	0.030 ± 0.004	0.012 ± 0.002	0.015 ± 0.002
Kernel depth, cm	0.007 ± 0.001	0.008 ± 0.001	0.005 ± 0.001	0.007 ± 0.001
Row number, no.	1.52 ± 0.22	1.20 ± 0.18	1.72 ± 0.25	1.54 ± 0.23
Grain yield, kg ha^{-1}	1208.5 ± 178.2	1473.4 ± 217.2	682.7 ± 100.7	921.3 ± 135.8
Days to silking, no.	6.95 ± 1.02	5.33 ± 0.79	2.08 ± 0.31	3.49 ± 0.51

[a]Expressed as the ratio of ear height to plant height.

Table A19. Phenotypic variance estimates among 100 S_1 progenies in the F_2 and F_2 Syn 5 generations derived from two single crosses evaluated at the Atomic Energy Center, 1985

Traits	Single crosses	
	B73 x Mo17	
	F_2	F_2 Syn 5
Root lodging, %	59.0 ± 8.7	68.6 ± 10.1
Stalk lodging, %	82.4 ± 12.2	131.5 ± 19.4
Dropped ears, %	0.11 ± 0.02	0.23 ± 0.03
Plant height, cm	149.6 ± 22.1	139.8 ± 20.6
Ear height, cm	91.3 ± 13.5	102.3 ± 15.1
Ear length, cm	1.72 ± 0.25	1.51 ± 0.22
Ear diameter, cm	0.058 ± 0.009	0.042 ± 0.006
Cob diameter, cm	0.023 ± 0.003	0.018 ± 0.003
Ear index[a]	0.00095 ± 0.00014	0.0015 ± 0.0002
Prolificacy, no.	0.013 ± 0.002	0.024 ± 0.004
Kernel depth, cm	0.0087 ± 0.0013	0.0075 ± 0.0011
Row number, no.	1.50 ± 0.23	1.22 ± 0.18
Grain yield, kg ha^{-1}	960.8 ± 141.7	1149.7 ± 169.5
Days to silking, no.	6.60 ± 0.97	5.01 ± 0.74

[a]Expressed as the ratio of ear height to plant height.

Single crosses	
B73 x B84	
F_2	F_2 Syn 5
161.9 ± 23.9	134.8 ± 19.9
24.2 ± 3.6	36.1 ± 5.3
0.17 ± 0.03	0.11 ± 0.02
97.3 ± 14.3	105.2 ± 15.5
66.6 ± 9.8	71.9 ± 10.6
1.18 ± 0.17	1.77 ± 0.26
0.026 ± 0.004	0.035 ± 0.005
0.013 ± 0.002	0.013 ± 0.002
0.00094 ± 0.00014	0.0012 ± 0.0002
0.008 ± 0.001	0.015 ± 0.002
0.0055 ± 0.0008	0.0084 ± 0.0012
1.60 ± 0.24	1.32 ± 0.20
689.0 ± 101.6	896.1 ± 132.1
4.54 ± 0.67	4.31 ± 0.64

APPENDIX B. COMPUTER PROGRAM TO OBTAIN CORRELATIONS

Matrix program to estimate genetic and phenotypic correlations.

```
//NAME  JOB I3757,ZACATECAS
//S1 EXEC SAS
//SYSIN DD *
PROC MATRIX;
E = (YOUR E MATRIX FROM THE MANOVA OUTPUT)
    i.e. 1  2  3  4  5  6/                        ALL YOUR TRAITS
         .. .. .. .. .. ..;
H = (YOUR H MATRIX FROM THE MANOVA OUTPUT)
    i.e. 1  2  3  4  5  6/
         .. .. .. .. .. .. ;
SH=1#/SQRT(DIAG(H));                          Calculate phenotypic cor-
CH=SH * H * SH;                                 relation;
NR=NROW(H);                                   Number of rows;
NC=NCOL(H);                                   Number of columns;
TH=J(NR,NC);
PH=TH;
DO I1=1 TO NR;
IP1=I1+1;
DO I2=IP1 TO NC;
TH(I1,I2)=(CH(I1,I2)*SQRT(d.f.))#/SQRT(1-CH(I1,I2)**2;
TH(I2,I1)=TH(I1,I2);                                        Significance
PH(I1,I2)=(1-PROB(ABS(TH(I1,I2)),d.f.))*2;                  test;
PH(I2,I1)=PH(I1,I2);
END;
END;
PRINT H CH PH;
D=H-E;
GH=1#/SQRT(DIAG(D));
CG=GH*D*GH;                                 Calculate genetic correlation;
DO I3=1 TO NR;
CG(I3,I3)=1;
END;
PRINT E CG;
/*
//
```